MALACOLOGIA, 2011, 53(2): 279–363

A SURVEY OF VITRINID LAND SNAILS (GASTROPODA: PULMONATA: LIMACOIDEA)

Folco Giusti*, Viviana Fiorentino, Andrea Benocci & Giuseppe Manganelli

Dipartimento di Scienze Ambientali, Università di Siena, Via Mattioli 4, I-53100 Siena, Italy

ABSTRACT

There is general agreement that the vitrinids, a mainly Palaearctic group of semislugs, are higher stylommatophorans, but uncertainty still exists about their relationships. We therefore conducted a phylogenetic study based on morphological characters to determine relationships between genus-group taxa and to test monophyly and revise current taxonomy. Eighteen genus-group taxa – those listed as valid in the recent literature plus the new genus *Azorivitrina* – were considered using an exemplar approach, with individual species as terminals to avoid *a priori* assumption of monophyly. At least two species, one of which was the type species, were examined when possible. Phylogenetic analyses were performed using different outgroups consisting of a selection of western Palaearctic limacoidean genera (data partition I, DPI: outgroup consisting of *Euconulus*, *Deroceras, Oxychilus*, *Tandonia*, *Vitrea* and *Troglaegopis*; DPII: outgroup *Euconulus*, *Oxychilus*, *Vitrea* and *Troglaegopis*; DPIII: outgroup *Euconulus* and *Oxychilus*). Different approaches were used: parsimony analysis (MP: using PAUP* 4.0; AP: TNT software) and bayesian inference (BI: using MRBAYES). Phylogeny analysis generally had low resolution. The parsimony analysis using implied weights (TNT software) provided the best results (AP found 11 supported clades, MP 11 and BI 8). It did not support monophyly of most genus-group taxa or the monophyletic groups found by Hausdorf (1995, 2002) and Alonso et al. (2000), or the subfamilies and tribes established by Schileyko (1986, 2003), or the family Vitrinidae when the outgroup consisted of a large selection of limacoidean taxa. Support was only found for *Canarivitrina*, *Guerrina*, *Oligolimax* and *Vitrinobrachium* and some support for *Arabivitrina* and *Azorivitrina*. On the contrary, no support was found for *Eucobresia*, *Insulivitrina* and *Phenacolimax*, or for *Plutonia sensu* Alonso et al. (2000). The most resolved group (but with low support values) was a clade including species of *Oligolimax*, *Sardovitrina*, *Semilimacella* and *Vitrina* supported by exclusive disposition of the penial retractor above the right ommatophore retractor. These results indicate that a different approach to vitrinid phylogeny and systematics is needed because morphological characters alone do not generate a realistic picture. In the meantime, we ranked the 18 genus-group taxa as distinct genera, although we are perfectly aware that some may be paraphyletic or polyphyletic.

Finally we concisely surveyed all vitrinid genera, listing them in three distinct groups according to stimulator structure: vitrinids with vaginal stimulator (glandula amatoria); vitrinids with diverticular stimulator (atrial/atrial-vaginal/vaginal or penial diverticular stimulator); vitrinids without vaginal or diverticular stimulator. This approach enables easy comparison of taxa with similar distal genital structure and is not intended to have any systematic or phylogenetic value. A short diagnosis of each taxon is given together with re-description of the type species and remarks.

Key words: Vitrinidae, phylogeny, systematics, character evolution, description of new taxa.

INTRODUCTION

In recent years, the vitrinids have received much attention (Groh & Hemmen, 1986; Schileyko, 1986, 1991; Alonso et al., 1987, 2000; Ibáñez et al., 1987, 2001; Morales et al., 1988; Valido et al., 1990, 1993, 2000; Hausdorf, 1995, 2002; Wiktor & Backeljau, 1995; Neubert, 1998; Manganelli & Giusti, 2004, 2005; Nardi et al., 2007). Most of these contributions, however, have been concerned with taxonomy (revision of taxa and description of new genera/

---

*Corresponding author: giustif@unisi.it

subgenera and species); only Hausdorf (1995, 2002) and Alonso et al. (2000) investigated their internal phylogeny.

Hausdorf (1995) used a cladistic approach to explore the relationships of the new species *Gallandia olympica* with *Gallandia annularis* and *Trochovitrina lederi,* using *Insulivitrina* as outgroup. He found that these three taxa constitute a monophyletic group (*G. annularis* (*G. olympica*, *T. lederi*)) and consequently regarded *Trochovitrina* as a junior synonym of *Gallandia* (the latter in turn is a junior synonym of *Oligolimax*; Manganelli & Giusti, 2004).

Alonso et al. (2000) analyzed the relationships of the "plutoniine" vitrinids (*Arabivitrina*, *Canarivitrina*, *Gallandia*, *Guerrina*, *Insulivitrina*, *Madeirovitrina*, *Phenacolimax* and *Plutonia*) using *Semilimax* as outgroup. They found eight equally parsimonious trees with a largely unresolved strict consensus tree (*Semilimax* (*Phenacolimax* (*Arabivitrina*, *Canarivitrina*, *Gallandia*, *Guerrina*, *Insulivitrina*, *Madeirovitrina*, *Plutonia*))). They adopted a largely unresolved tree (*Semilimax* (*Phenacolimax* (*Arabivitrina*, *Gallandia* (*Canarivitrina*, *Guerrina*, *Insulivitrina*, *Madeirovitrina*, *Plutonia*)))) as the preferred phylogenetic hypothesis and accordingly regarded all Macaronesian taxa (*Canarivitrina*, *Guerrina*, *Insulivitrina*, *Madeirovitrina* and *Plutonia*) as subgenera of *Plutonia*.

Hausdorf (2002) analyzed the phylogeny of all the genera assigned to the family, using *Troglaegopis* Riedel & Radja, 1983 (Zonitidae, Zonitoidea) and *Cryptozona* Mörch, 1872 (Ariophantidae, Helicarionoidea) as outgroups. On the basis of a character matrix of 12 taxa and 17 characters, he found two equally parsimonious trees which gave the following strict consensus tree: (*Semilimax*, *Vitrinobrachium* ((*Semilimacella*, *Vitrina*) (*Eucobresia* (*Phenacolimax* ((*Plutonia*, *Oligolimax*) (*Arabivitrina*, *Calidivitrina*)))))). Unfortunately, Hausdorf's phylogenetic study has some shortcomings due to the fact that he used supraspecific taxa whose monophyly was implicitly assumed, scored characters partly from the literature and did not calculate any statistical support to clades.

We therefore conducted a new phylogenetic study on the basis of the morphological characters of all the valid genus-group taxa using an exemplar approach. The aim was: (1) to investigate relationships between genus-group taxa, (2) to test their monophyly, and (3) to revise current taxonomy.

MATERIAL AND METHODS

Taxonomic Sample

Hausdorf (2002) and Schileyko (2003) proposed the most recent supraspecific classification of the family Vitrinidae (Table 1). Although the number of genus-group taxa is almost equivalent (14 according to Hausdorf vs. 15 according to Schileyko), the arrangement is quite different. First of all, Schileyko continued to use *Oligolimax* in the sense of Forcart (1965) for *Semilimacella* and assigned species included in *Oligolimax* by all other authors to *Phenacolimax*. As proposed by Alonso et al. (2000), Hausdorf accepted that the Macaronesian vitrinids belong to a polytypic genus (*Plutonia*, with five subgenera: *Canarivitrina*, *Guerrina*, *Insulivitrina*, *Madeirovitrina* and *Plutonia* s.s.), whereas Schileyko assigned them to four distinct genera (*Guerrina*, *Insulivitrina*, *Madeirovitrina* and *Plutonia*), one of which was polytypic (*Plutonia*, with two subgenera: *Canarivitrina* and *Plutonia* s.s.). Finally Hausdorf regarded *Hessemilimax* (a subgenus of *Semilimax*, according to Schileyko) and *Trochovitrina* (a distinct genus, according to Schileyko) as junior synonyms of *Semilimax* and *Oligolimax*, respectively.

Our analysis considered all the genus-group taxa listed as valid by Hausdorf and Schileyko plus *Sardovitrina* recently described by us (Manganelli & Giusti, 2004) and the new genus *Azorivitrina* (Table 1), making a total of 18 taxa of the genus group. In order to avoid *a priori* assumption of monophyly of supraspecific taxa, an exemplar approach with individual species as terminals was used (Prendini, 2000). Consequently at least two species, one of which was the type species, were examined, when possible, for each polytypic genus-group taxon.

Morphological Study

For each species considered, detailed anatomical re-examination was performed on the available material. The bodies were isolated removing them from the shells and dissected under the light microscope (Wild M5A) using very fine pointed watchmaker's tweezers. Anatomical details were drawn using a Wild camera lucida.

The material examined is listed as follows, when possible: locality, municipality and province names in parenthesis, UTM reference,

TABLE 1. Classification of the vitrinids according to Hausdorf (2002) and Schileyko (2003) and taxa of the genus group considered in the present survey.

Hausdorf (2002)	Schileyko (2003)	Taxa considered in the present survey
Vitrinidae Fitzinger, 1833	**Vitrinidae Fitzinger, 1833**	**Vitrinidae Fitzinger, 1833**
Arabivitrina Thiele, 1931	**Plutoniainae Cockerell, 1893**	*Arabivitrina* Thiele, 1931
Calidivitrina Pilsbry, 1919	*Arabivitrina* Thiele, 1931	*Azorivitrina* n. gen.
Eucobresia Baker, 1929	*Insulivitrina* Hesse, 1923	*Calidivitrina* Pilsbry, 1919
Oligolimax Fischer in: Paulucci, 1878	*Phenacolimax* Stabile, 1859	*Canarivitrina* Valido & Alonso in: Alonso et al., 2000
Phenacolimax Stabile, 1859	*Trochovitrina* Boettger, 1880	*Eucobresia* Baker, 1929
Plutonia Stabile, 1864	*Plutonia* Stabile, 1864	*Guerrina* Odhner, 1954
Canarivitrina Valido & Alonso in: Alonso et al., 2000	*Canarivitrina* Valido & Alonso in: Alonso et al., 2000	*Hessemilimax* Schileyko, 1986
Guerrina Odhner, 1954	*Plutonia* s.s. Stabile, 1864	*Insulivitrina* Hesse, 1923
Insulivitrina Hesse, 1923	*Guerrina* Odhner, 1954	*Madeirovitrina* Groh & Hemmen, 1986
Madeirovitrina Groh & Hemmen, 1986	*Madeirovitrina* Groh & Hemmen, 1986	*Oligolimax* Fischer in: Paulucci, 1878
Plutonia s.s. Stabile, 1864	**Semilimacinae Schileyko, 1986**	*Phenacolimax* Stabile, 1859
Semilimacella Soós, 1917	**Oligolimacini Schileyko, 2003**	*Plutonia* Stabile, 1864
Semilimax Stabile, 1859	*Oligolimax* Fischer in: Paulucci, 1878	*Sardovitrina* Manganelli & Giusti, 2005
Vitrina Draparnaud, 1801	**Semilimacini Schileyko, 1986**	*Semilimax* Stabile, 1859
Vitrinobrachium Künkel, 1929	*Semilimax* Stabile, 1859	*Semilimacella* Soós, 1917
	Semilimax s.s. Stabile, 1859	*Trochovitrina* Boettger, 1880
	Hessemilimax Schileyko, 1986	*Vitrina* Draparnaud, 1801
	Vitrinobrachium Künkel, 1929	*Vitrinobrachium* Künkel, 1929
	Eucobresia Baker, 1929	
	Vitrininae Fitzinger, 1833	
	Calidivitrina Pilsbry, 1919	
	Vitrina Draparnaud, 1801	

collector(s), date, number of specimens and collection in which material is kept in parenthesis. Key to acronyms used in material examined: FGC, F. Giusti collection (Dipartimento di Scienze Ambientali, Università di Siena, Siena, Italy); IRSNB, Institut Royal des Sciences Naturelles de Belgique (Brussels, Belgium); MNHN, Muséum National d'Histoire Naturelle (Paris, France); NHMW, Naturhistorisches Museum Wien (Vienna, Austria); SMF, Senckenberg-Museum (Frankfurt am Main, Germany); ZMMU, Zoological Museum of Moscow University (Moscow, Russia).

Key to acronyms used in figures: A, atrium; AAVS, apical portion of atrial-vaginal stimulator; AG, albumen gland; AP, accessory pilaster; AS, atrial stimulator; ASC, atrial semicircular crest; AVS, apical portion of vaginal stimulator; BAVS, basal portion of atrial-vaginal stimulator; BC, bursa copulatrix; BVS, basal portion of vaginal stimulator; BW, body wall; CS, coagulated secretion; CSS, conical structure of stimulator; DBC, duct of bursa copulatrix; DV, distal vagina; EGL, external glandular layer; FHD, first hermaphrodite duct; FO, free oviduct; G, gonad; GA, glandula amatoria; GN, genital nerve; GR, glandular roll; IGL, internal glandular layer; L, lumen; LGR, lamellate portion of glandular roll; MP, main pilaster; MS, muscular strips; OSD, ovispermiduct; PAVS, papilla of atrial-vaginal

TABLE 2. Character matrix used for the phylogenetic analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Deroceras laeve (Müller, 1774)	2	0	0	1	0	-	0	1	0	0	1	-	1	1	-	-	2	0	0	0	0	-	-	-	1
Euconulus fulvus (Müller, 1774)	0	1	0	0	2	-	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Oxychilus cellarius (Müller, 1774)	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	-	-	-	0
Tandonia budapestensis (Hazay, 1881)	2	1	0	0	0	-	0	0	0	0	1	-	0	1	-	-	0	0	0	0	0	-	-	-	1
Troglaegopis mosorensis (Kuščer, 1933)	0	0	1	0	2	-	0	1	0	0	1	-	0	1	-	-	1	0	0	0	0	1	1	1	0
Vitrea crystallina (Müller, 1774)	0	0	0	0	0	-	0	1	0	1	0	0	0	1	-	-	1	0	0	0	0	-	-	-	1
Arabivitrina arabica (Thiele, 1910)	1	1	0	0	1	0	1	1	0	0	0	0	2	1	-	-	1	1	0	0	0	-	-	-	2
Arabivitrina jansseni Neubert, 1998	1	1	0	0	1	0	1	1	0	0	0	0	2	1	-	-	1	1	0	0	0	-	-	-	2
Azorivitrina brevispira (Morelet, 1860)	1	1	0	0	0	-	0	1	0	0	0	1	2	1	-	-	2	0	0	0	1	-	-	-	2
Azorivitrina finitima (Morelet, 1860)	1	1	0	0	1	0	1	1	0	0	0	1	2	0	?	2	1	0	0	0	1	-	-	-	2
Azorivitrina laxata (Morelet, 1860)	1	1	0	0	1	0	1	1	0	0	0	1	2	1	-	-	1	1	0	0	1	-	-	-	2
Canarivitrina dianae (Valido & Alonso in: Alonso et al., 2000)	1	1	0	0	1	0	1	1	0	0	0	1	2	1	-	-	3	0	1	0	0	-	-	-	2
Canarivitrina taburientensis (Groh & Valido in: Alonso et al., 2000)	1	1	0	0	1	0	1	1	0	0	0	1	2	1	-	-	3	0	1	0	0	-	-	-	1
Guerrina christinae Groh in: Valido et al., 1993	0	1	0	0	1	1	1	1	0	0	0	1	2	1	-	-	2	1	0	0	0	-	-	-	1
Guerrina cuticula (Shuttleworth, 1852)	0	1	0	0	1	1	1	1	0	0	0	1	2	1	-	-	2	1	0	0	0	-	-	-	2
Insulivitrina eceroensis Alonso & Ibáñez, 1987	1	1	0	0	1	0	1	1	0	0	0	1	2	1	-	-	2	0	0	0	0	-	-	-	1
Insulivitrina lamarckii (Férussac, 1821)	1	1	0	0	1	0	1	1	0	0	0	1	2	0	1	2	1	0	0	0	0	-	-	-	2
Madeirovitrina marcida (Gould, 1847)	1	1	0	0	1	0	1	1	0	0	0	1	2	1	-	-	2	1	0	1	0	-	-	-	2
Madeirovitrina nitida (Gould, 1847)	1	1	0	0	1	0	1	1	0	0	0	1	2	1	-	-	2	1	0	1	0	-	-	-	2

(continues)

(continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Oligolimax annularis (Studer, 1820)	0	1	0	0	1	1	1	1	0	0	1	-	2	1	-	-	1	0	0	0	0	-	-	-	1
Oligolimax musignani (Pirajno, 1842)	0	1	0	0	1	1	1	1	0	0	1	-	2	1	-	-	1	0	0	0	0	-	-	-	1
Phenacolimax blanci (Pollonera, 1884)	1	1	0	0	1	1	1	1	0	0	0	0	2	0	0	2	1	0	0	0	0	-	-	-	2
Phenacolimax major (Férussac, 1807)	1	1	0	0	1	1	1	1	0	0	0	0	2	0	1	2	1	0	0	0	0	-	-	-	0
Plutonia atlantica (Morelet, 1860)	2	1	0	0	1	0	1	1	1	0	-	-	2	1	-	-	1	0	0	0	0	-	-	-	2
Sardovitrina polloneriana ([Arbanasich], 1897)	1	1	0	0	1	1	1	1	0	0	1	-	2	1	-	-	1	0	0	0	0	-	-	-	2
Trochovitrina lederi (Boettger, 1878)	1	?	-	0	1	0	0	1	0	0	?	?	2	1	-	-	2	0	0	0	0	-	-	-	1
Hessemilimax kotulae (Westerlund, 1883)	1	1	0	0	2	-	0	1	0	0	0	1	2	0	0	2	2	0	0	0	0	2	1	1	2
Semilimacella bonelli (Targioni Tozzetti, 1873)	1	1	1	0	2	-	0	1	0	0	1	-	2	0	0	2	1	0	0	0	0	1	1	3	1
Semilimacella cephalonica (Rähle, 1980)	1	?	0	0	2	-	0	1	0	0	1	-	2	0	0	2	2	0	0	0	0	1	1	1	1
Semilimax carinthiacus (Westerlund, 1886)	1	1	0	0	2	-	0	1	0	0	0	1	2	0	0	2	1	0	0	0	0	2	1	2	2
Semilimax pyrenaicus (Férussac, 1821)	1	1	0	0	2	-	0	1	2	-	-	-	2	0	0	2	1	0	0	0	0	2	1	1	2
Semilimax semilimax (Férussac, 1802)	1	1	0	0	2	-	0	1	2	-	-	-	2	0	0	2	1	0	0	0	0	2	1	2	2
Vitrinobrachium baccettii Giusti & Mazzini, 1971	1	1	0	1	2	-	0	1	0	1	0	0	2	0	1	2	1	0	0	0	0	1	0	4	2
Vitrinobrachium breve (Férussac, 1821)	1	1	0	1	2	-	0	1	0	1	0	0	2	0	1	2	1	0	0	0	0	1	0	4	2
Calidivitrina cf. *oleosa* (Martens, 1895)	1	?	0	0	0	-	3	1	0	0	?	?	2	1	-	-	2	1	0	0	0	-	-	-	2
Eucobresia diaphana (Draparnaud, 1805)	1	1	0	0	0	-	3	1	0	0	0	0	2	0	1	2	1	0	0	0	0	-	-	-	1
Eucobresia glacialis (Forbes, 1837)	1	1	0	0	1	1	1	1	0	0	0	0	2	0	1	2	1	0	0	0	0	-	-	-	1
Eucobresia nivalis (Dumont & Mortillet, 1852)	1	1	0	0	0	-	2	1	0	0	0	0	2	0	1	2	1	1	0	0	0	-	-	-	2
Vitrina pellucida (Müller, 1774)	1	1	1	0	0	-	0	1	0	0	1	-	2	0	1	2	1	0	0	0	0	-	-	-	2

stimulator; PC, penial complex; PG, penial gland; PGA, papilla of glandula amatoria; PLC, penial laminar crest; PLS, papilla-like structure; PN, penial nerve; POS, prostatic portion of ovispermiduct; PR, penial retractor muscle; PS, penial sheath; PST, penial stimulator; SPS, pedunculate sucker of stimulator; T, talon; TLS, tongue-like structure; UOS, uterine portion of ovispermiduct; V, vagina; VD, vas deferens; VDO, vas deferens opening; VLC, vaginal laminar crest; VLP, vaginal longitudinal pilaster/pleat; VP, vaginal papilla; VW, vaginal walls.

In the anatomical description the use of directional (proximal and distal; basal and apical) and descriptive terms (short vs. long, slender vs. wide, etc.) was applied as follows. In the case of the ducts of the main axis of the genitalia (e.g., free oviduct, vagina, vas deferens, penial complex, etc.), proximal denotes the part which is closer to the gonad and distal the part which is closer to the gonopore. In the case of the blind structures radiating from the main axis of the genitalia (bursa copulatix complex, penial/vaginal/atrial appendix, etc.), basal or initial denotes the part closer to, and apical or terminal the part further from the main axis of the genitalia; in the case of the penial sheath, basal or initial denotes the part closer to, and apical or terminal the part further from where the sheath joins the penial complex. The descriptive terms (e.g., short vs. long, slender vs. wide, etc.) refer to comparisons of the same tract of the genitalia in different taxa. Unfortunately, only extreme cases are easy to evaluate; intermediate cases are very difficult to evaluate objectively due to large variability between taxa. Application of these simple categories is far from banal. Apparently simple structures (penial complex or even bursa copulatrix, duct of bursa copulatix, etc.) may be so different in different taxa as to elude any attempt at objective comparison. Besides variability between taxa, sometimes variations may be due to different sexual maturation of reproductive organs, fixation, and in the case of drawings in the literature, different fidelity of illustration. Only examination of a considerable number of specimens by the same researcher would provide real insights, but this was not possible due to unavailability of material.

Characters

Twenty-five characters (Table 2) were scored during examination of 33 species belonging to the in-group. Other potential characters were considered (e.g., penial complex length, distal vagina length, bursa copulatrix shape), but in the end they were disregarded due to the difficulty of coding and evaluating (see morphological study). Other characters recently used for phylogenetic analysis of the vitrinids, or of limacoideans, are sole, spermatophore, sexual behaviour and radula (see: Muratov, 1999; Hausdorf, 2002). Although they are interesting, we excluded them because data was only available for a handful of species.

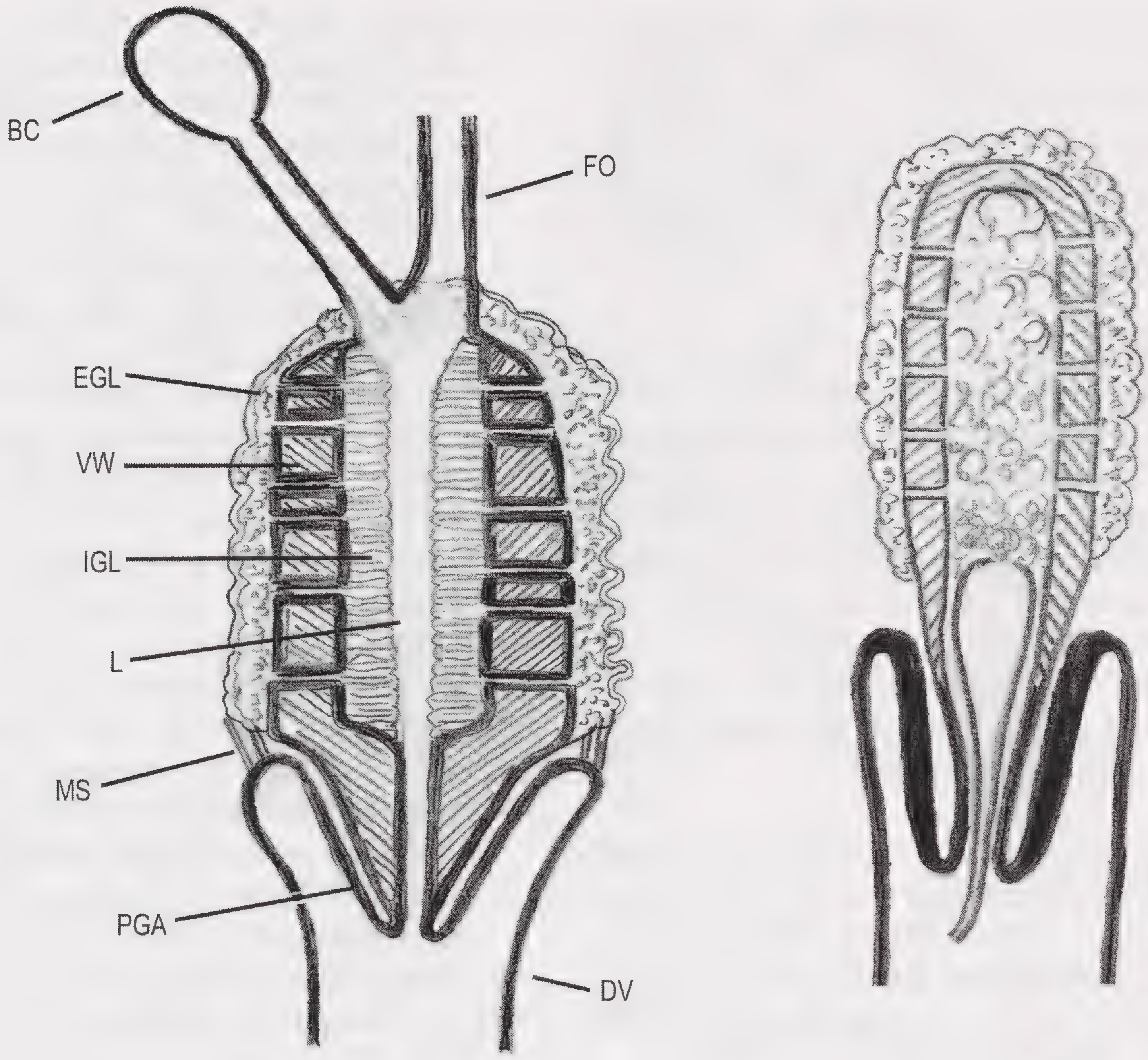
1. *Habitus*: 0 = snail-like (animal can completely withdraw into shell); 1 = semislug-like (the animal cannot completely withdraw into shell); 2 = slug-like. State 2 is unique to *Plutonia atlantica*. This character was also used by Alonso et al. (2000: tables 2, 3, character 1 "Shell"), but not by Hausdorf (2002).

2. *Penial innervation*: 0 = from cerebral ganglion; 1 = from pedal ganglion. State 0 is found in *Deroceras laeve* (Hausdorf, 1998: table 3, character 14, as Agriolimacidae), *Oxychilus cellarius*, *Vitrea crystallina* (Hausdorf, 1998: table 3, character 14, as Vitreidae) and *Troglaegopis mosorensis*; state 1 is found in *Euconulus fulvus*, *Tandonia budapestensis* and all the vitrinids examined.

3. *Bursa copulatrix duct*: 0 = initially not or only slightly flared; 1 = initially much flared. State 1 is only found in *Troglaegopis mosorensis*, *Semilimacella bonelli* and *Vitrina pellucida*. This character is not applicable to *Trochovitrina lederi* which apparently lacks bursa copulatrix.

4. *Vagina*: 0 = present; 1 = absent (vagina is absent when duct of bursa copulatrix is attached to penial complex). State 1 is only found in *Deroceras laeve* and species of *Vitrinobrachium.*

5. *Stimulator structures* (Figs. 1, 2): 0 = absent; 1 = glandula amatoria; 2 = diverticular stimulator. For other characters scored on diverticular stimulator, see nos. 22–24. Stimulator characters were also used by Alonso et al. (2000: tables 2, 3, character 3 "Location of the glandula amatoria – stimulator organ": 0 = distinct from vagina; 1 = fused to the proximal part of vagina) and Hausdorf (2002: table 1, character 1 "Stimulator": 0 = present; 1 = missing; character 2 "Stimulator": 0 = inserts laterally



FIGS. 1, 2. Vitrinid stimulator structures. FIG. 1: Glandula amatoria; FIG. 2: Diverticular stimulator (based on that of *Semilimax semilimax*).

at atrium or vagina; 1 = completely fused with vagina). There is general agreement that the various types of stimulator of the vitrinids are homologous (Schileyko, 1986; Hausdorf, 1998, 2002), but different assumptions have been made about their evolution. Hausdorf (1998, 2002) believed that the diverticular stimulator was primitive and that the vaginal stimulator (glandula amatoria) originated by fusion of it with the vagina. On the contrary Schileyko (1986) considered the glandula amatoria the primitive form of stimulator, directly derived from a sort of vaginal gland; in differentiating from the vagina, the glandula amatoria allegedly gave rise to the atrial/penial stimulator. We accepted the hypothesis that the vitrinid stimulators are homologous, but avoided any polarity assumption.

6. *External glandular covering of glandula amatoria*: 0 = uniform and complete or almost complete; 1 = reduced. This character is not applicable to taxa lacking glandula amatoria (see character 5). A continuous complete (or almost complete) external glandular covering of glandula amatoria is found in species of *Arabivitrina*, *Canarivitrina*, *Insulivitrina*, *Madeirovitrina*, *Plutonia* and *Trochovitrina*, whereas a reduced, incomplete external glandular covering is present in species of *Eucobresia*, *Guerrina*, *Phenacolimax*, *Oligolimax* and *Sardovitrina*. Simple glandular covering, not associated with a glandula amatoria, is also present around proximal vagina of *Oxychilus cellarius*, *Semilimacella bonelli* and *Vitrina pellucida*.

Hausdorf (2002) regarded the external glandular covering of glandula amatoria and that of appendicular stimulators as homologous and scored on it three characters, according to presence vs. absence (character 3: 0 = present; 1 = absent), length (character 4: 0 = distinctly longer than wide; 1 = about as long as or shorter than wide) and extension around proximal portion of vaginal stimulator or apical portion of diverticular stimulator (character 5: 0 = uniform sheath around proximal stimulator portion; 1 = divided into lobes). However, it is impossible to compare these structures in relation to the extent of their covering (one is a cylinder and the other a cup).

7. *Vaginal papilla*: 0 = absent; 1 = present; 2 = reduced; 3 = very reduced. A conical vaginal papilla is found in all vitrinids with glandula amatoria apparently except *Trochovitrina lederi*. A small proximal vaginal papilla is present in *Eucobresia nivalis* and a pleated proximal annular pad in *Calidivitrina* cf. *oleosa* and *Eucobresia diaphana*. The vaginal pad may actually be an extreme reduction of the glandula amatoria of a *Phenacolimax*-like ancestor.

8. *Epiphallus*: 0 = present; 1 = absent. State 0 subsists in *Euconulus fulvus*, *Oxychilus cellarius* and *Tandonia budapestensis*; state 1 in *Deroceras laeve*, *Troglaegopis mosorensis*, *Vitrea crystallina* (Barker, 1999: 117) and all the vitrinids examined.

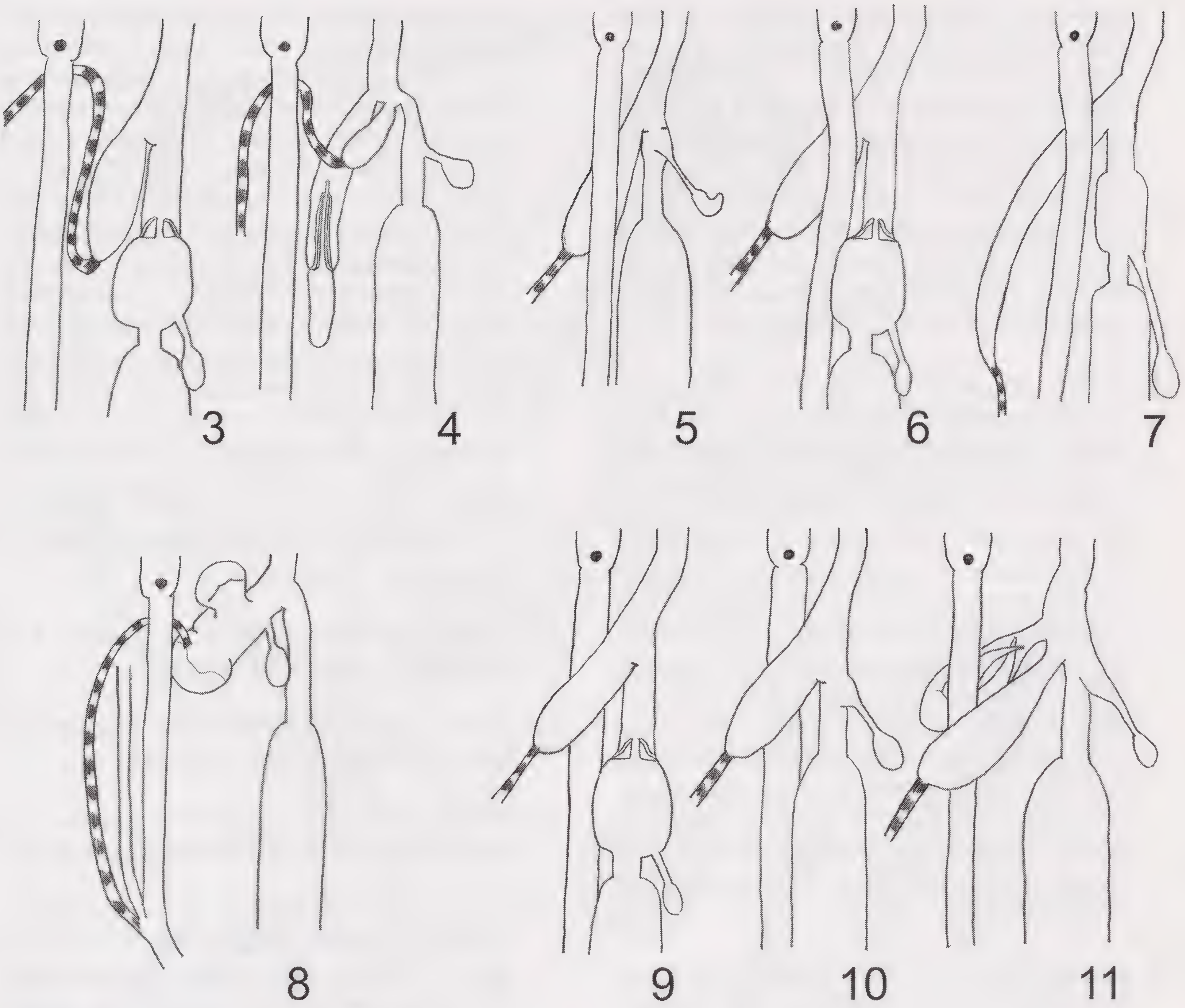
9. *Penial retractor*: 0 = present; 1 = subdivided into three branches, none of which reaches penial complex (the first reaches bursa copulatrix and its duct, second free oviduct and third vas deferens); 2 = absent. State 1 is only found in *Plutonia atlantica* and state 2 in two species of *Semilimax* (*S. semilimax* and *S. pyrenaicus*).

10. *Origin of penial retractor*: 0 = penial retractor from diaphragm; 1 = penial retractor from columellar muscle. State 1 is found in *Vitrea crystallina* (Barker, 1999: 117) and *Vitrinobrachium* species. This character is not applicable to taxa without penial retractor (see character 9) and was codified by Hausdorf (2002: table 1, character 14 "Insertion site of the penial retractor muscle") in the same way.

11. *Right ommatophore retractor and penial retractor in adults* (Figs. 3–11): 0 = ROR above PR/PC; 1 = ROR below PR/PC. As in the case of characters 9–10, this character is not applicable to taxa with modified or no PR (see character 9). When PR is short, PC is displaced left and located below or above ROR. In the first case (ROR above PC: adults of *Arabivitrina*, *Eucobresia* and *Phenacolimax*), PR does not have an S-like course around the optic nerve and ROR passes between penial complex and vagina. In the second case (ROR below PC: species of *Oligolimax*, *Sardovitrina*, *Semilimacella* and *Vitrina*), ROR runs free of both optic nerve and distal genitalia. When PR is long and has an S-like course around the optic nerve (juveniles of *Arabivitrina*, *Eucobresia* and *Phenacolimax* and juveniles and adults of all Macaronesian vitrinids, *Semilimax* and *Vitrinobrachium*), ROR passes far left of PC and above PR (see character 12).

This character was codified by Alonso et al. (2000: tables 2, 3, character 7 "Arrangement of the penial retractor muscle") in three states: 0 = PR free of right optic nerve [= ROR below PR]; 1 = PR passing around right optic nerve [= ROR above PR]; 2 = PR absent (*Plutonia*) and by Hausdorf (2002: table 1, character 13 "Right ommatophore retractor muscle") in two states: 0 = ROR runs left of or below PR (ROR can be moved to left without affecting PR); 1 = ROR runs right of or above PR (ROR cannot be moved to left without affecting PR). In both cases, their state 0 corresponds to our state 1 and vice versa (our codification depends on the fact that we listed *Oxychilus* (0) as first outgroup). Alonso et al. (2000) assigned state 0 to *Arabivitrina* and *Semilimax* (PR free of right optic nerve) but this is a mistake.

12. *Right ommatophore retractor and penial retractor in adults when ROR is above PR* (Figs. 3–11): 0 = PR short, PC shifted left and ROR between distal genitalia (species of *Arabivitrina*, *Eucobresia*, *Phenacolimax*); 1 = PR long and with S-like course around optic nerve, PC located right and ROR not between distal genitalia. The position of ROR with respect to the distal genitalia depends on the length of PR which may change between juveniles and adults of some genera (see *Arabivitrina* and *Phenacolimax*). This character was also considered by Hausdorf (2002: table 1, character 12 "Right ommatophore retractor muscle") and codified in this way: 0 = ROR does not pass between penis and the female genitalia (ROR can be moved to left



FIGS. 3–11. Scheme of relationships between distal genitalia, penial retractor and right ommatophore retractor. FIG. 3: *Canarivitrina*, *Guerrina*, *Insulivitrina* and *Madeirovitrina* and juveniles of *Arabivitrina* and *Phenacolimax*; FIG. 4: *Semilimax*; FIG. 5: *Eucobresia*; FIG. 6: *Calidivitrina* and adults of *Arabivitrina* and *Phenacolimax*; FIG. 7: *Oxychilus*; FIG. 8: *Vitrinobrachium*; FIG. 9: *Oligolimax* and *Sardovitrina*; FIG. 10: *Vitrina*; FIG. 11: *Semilimacella.*

without affecting the penis); 1 = ROR passes between penis and the female genitalia (ROR cannot be moved to left without affecting penis). We do not agree with this codification because ROR position with respect to distal genitalia cannot be compared in vitrinids with ROR above the PR/PC and those with ROR below PR/PC (see character 11). In fact Hausdorf erroneously considered the situations of *Oligolimax*, *Semilimacella* and *Vitrina* (short PR, ROR below the PC) and those of *Plutonia* (s. l.) and *Vitrinobrachium* (long PR, ROR above the PC) to be homologous.

13. *Penial gland*: 0 = absent; 1 = only distal; 2 = complete or only proximal. State 0 subsists in *Euconulus fulvus*, *Oxychilus cellarius*, *Tandonia budapestensis*, *Troglaegopis mosorensis* and *Vitrea crystallina*; state 1 is found in *Deroceras laeve*; state 2 in all vitrinids.

14. *Penial sheath*: 0 = present; 1 = absent. The penial sheath is absent in four species of the outgroup (*Deroceras laeve*, *Tandonia budapestensis*, *Troglaegopis mosorensis* and *Vitrea crystallina*), in species of *Calidivitrina*, *Arabivitrina*, *Oligolimax*, *Sardovitrina*, *Trochovitrina*

and all Macaronesian vitrinids except *Azorivitrina finitima*, *Insulivitrina blauneri* and *Insulivitrina lamarckii*. This character was also considered by Alonso et al. (2000: tables 2–3, character 6 “Penial sheath”) and Hausdorf (2002: table 1, character 8 “Penial tunica”). However Hausdorf (2002) erroneously assigned state 0 (penial sheath present) to *Troglaegopis*, possibly due to the fact that Zhiltsov & Selivanova (2000) called the penial wall “penial sheath”.

15. *Origin of penial sheath*: 0 = PS joins penial complex distally; 1 = PS joins penial complex medially. This character is not applicable to the taxa without penial sheath (see character 14). It was also used by Hausdorf (2002: table 1, character 9 “Penial tunica”) though differently codified: PS covering especially the distal penial complex (0: *Semilimacella*, *Semilimax*, *Vitrina* and *Vitrinobrachium*); PS covering the proximal penial complex (1: *Eucobresia* and *Phenacolimax*). Actually, the most important feature is not what the PS covers but the point where it joins the penial complex. In fact, PS is often wrinkled up, giving an erroneous impression of its real length (see for example, *Vitrina pellucida*: Figs. 103, 104).

16. *Penial sheath and vas deferens*: 0 = not traversed by vas deferens; 1 = apically traversed; 2 = basally traversed by vas deferens. State 0 is unique to *Euconulus fulvus.* State 1 is unique to *Oxychilus cellarius.* This character is not applicable to taxa lacking the penial sheath (see characters 14 and 15).

17. *Vas deferens entering penis*: 0 = vas deferens entering penial complex via epiphallus; 1 = vas deferens entering penial complex apically; 2 = vas deferens entering penial complex proximally/medially; 3 = vas deferens entering penial complex distally (*Canarivitrina* species). This character was also used by Hausdorf (2002: table 1, character 15 “Insertion of the vas deferens at the penis”) but differently codified: terminally (0: *Semilimacella* and *Vitrina*); subterminally or laterally (1: all the others).

18. *Main pilaster, glandular roll*: 0 = without a medial lamellate portion; 1 = with a medial lamellate portion. This character was also used by Hausdorf (2002: table 1, character 10 “Main pilaster in penis”) and similarly codified: without a short lamellate section or distal section divided (0: all taxa except *Arabivitrina*, *Calidivitrina* and *Plutonia* in part); with a short lamellate section and an undivided distal section (1: *Arabivitrina*, *Calidivitrina* and *Plutonia* in part). State 1 is clearly present in *Arabivitrina*, *Calidivitrina*, *Guerrina*, *Madeirovitrina* and in two species of *Plutonia sensu* Mordan & Martins (2001) (*P. laxata* and *P. pelagica*). A glandular roll (or its derivative), more or less distally pleated, is also present in *Canarivitrina*, *Eucobresia*, *Insulivitrina*, *Oligolimax* and *Phenacolimax*, but it is not clear whether it corresponds to the lamellate glandular roll of the other taxa.

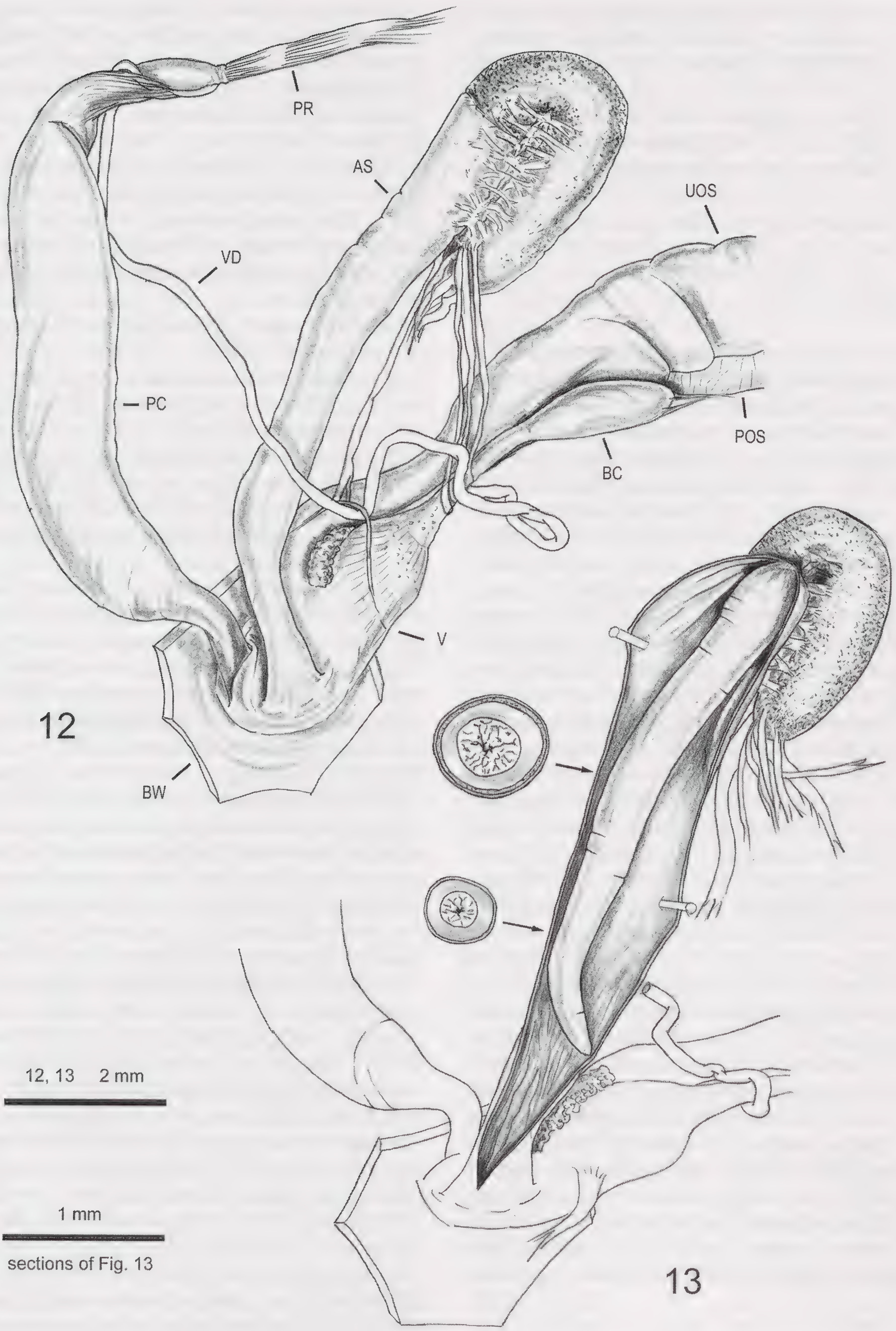
19. *Penial laminar crests*: 0 = absent; 1 = present (*Canarivitrina* species).

20. *Penial bridge-like pilaster*: 0 = absent; 1 = present (*Madeirovitrina* species).

21. *Penial pouch-like pilaster*: 0 = absent; 1 = present (Azorean “*Insulivitrina*” species).

22. *Diverticular stimulator*: 0 = finger-like without apical glandular portion; 1 = finger-like or club-like with apical glandular cap; 2 = finger-like or club-like with an apical pedunculated sac-like portion invaginated into basal portion. This character is not applicable to the taxa without stimulator structures (see character 5). Diverticular stimulators are present in *Euconulus fulvus*, *Troglaegopis mosorensis*, species of *Hessemilimax*, *Semilimax*, *Semilimacella* and *Vitrinobrachium* (Fig. 2). Contrary to what Hausdorf (2002) stated the external glandular covering of the apical portion of stimulator of *Semilimacella* is complete (it is perfectly equivalent to that of *Vitrinobrachium*).

23. *Diverticular stimulator location*: 0 = penial (penial stimulator); 1 = atrial or atrial-vaginal or vaginal (atrial/atrial-vaginal/vaginal stimulator). This character is not applicable to taxa without stimulator structures (see character 5). Hausdorf (2002) considered the stimulator of *Vitrinobrachium* to be atrial, whereas it is clearly penial.



FIGS. 12, 13. *Troglaegopis mosorensis* (Kuščer, 1933) from Špilja Vranjača, Kotlenica near Split (Croatia), A. Riedel leg. 11.5.1999. FIG. 12: Distal genitalia; FIG. 13: Internal structure and two transverse sections of atrial appendix.

24. *Diverticular stimulator internal structure*: 0 = absent; 1 = conical papilla; 2 = conical papilla with internal chitinous structure; 3 = two chitinous conical structures; 4 = fungiform papilla. This character is not applicable to the taxa without stimulator structures (see character 5).

25. *Genital atrium*: 0 = short; 1 = medium; 2 = long.

Outgroup

There is general agreement that the vitrinids are limacoideans, a group of higher pulmonates (Hausdorf, 1998; Wade et al., 2001, 2006). However, uncertainty still exists about their relationships (historical accounts: Forcart, 1956; Hausdorf, 1998, 2002; Muratov, 1999). According to a phylogeny of limacoideans based on morphological characters (Hausdorf, 1998), the vitrinids are limacoideans *sensu stricto*, being the sister group of boettgerillid, limacid and agriolimacid slugs. Recent phylogenies of a large series of stylommatophorans based on analysis of ribosomal (r) RNA gene cluster (Wade et al., 2001, 2006) confirmed that they are limacoideans, but their relationships are uncertain. Based on these phylogenies, we opted for a composite outgroup consisting of some west Palaearctic limacoidean genera examined by Wade et al. (2001, 2006) (*Euconulus*, *Deroceras, Oxychilus*, *Tandonia* and *Vitrea*) plus *Troglaegopis*. The latter (Figs. 12, 13) was included because it was used as outgroup by Hausdorf (2002) (actually Hausdorf used an outgroup of two taxa, but the second is the Indomalayan ariophantid *Cryptozona*).

Among the genera included in the outgroup, *Euconulus* and *Oxychilus* share a similarly structured penial sheath (namely a thin, short to long sac joined to a distal or medial constriction of the penial complex at one end and open at the other) with many vitrinids. Moreover, the penial sheath of the oxychiline zonitids and the vitrinids is uniquely traversed by vas deferens on one side (basally in the vitrinids, apically in oxychiline zonitids) and this makes the oxychiline zonitids the best candidate for a sister group of the vitrinids.

Phylogenetic Analysis

Several analyses were performed using different composite outgroups formed by six, four or two taxa: outgroup formed by *Euconulus*, *Deroceras, Oxychilus*, *Tandonia*, *Vitrea* and *Troglaegopis* (data partition I, DPI); outgroup formed by *Euconulus*, *Oxychilus*, *Vitrea* and *Troglaegopis* (data partition II, DPII); outgroup formed by *Euconulus* and *Oxychilus* (data partition III, DPIII).

Parsimony analyses were performed using PAUP* 4.0 (Swofford, 2003) (MP analyses) and TNT (Tree analysis using New Technology) software (Goloboff et al., 2003) (AP analyses).

Parsimony analyses using PAUP* were carried as follows:

(1) characters unordered, equal weight of character states;
(2) characters unordered, equal weight of characters (regardless of number of character states);
(3) characters unordered, equal weight of character states except for: characters 11, 12, 19, 20 and 21, each weighted 20 times (arbitrarily, see Discussion) for DPI, DPII and DPIII.

Heuristic searches under equal weight of all characters were performed with the following options: 1,000 random stepwise additions; TBR branch swapping; saving only optimal trees over all replicates; no more than 100 trees at each replicate. To evaluate clade support, nonparametric bootstrap resampling was used (1,000 replicates).

A traditional search was run in TNT, with these options: heuristic searches using multiple random addition sequences and/or branch swapping. Shortest trees were found by processing 2000 different addition sequences by the tree bisection-reconnection branch-swapping method (TBR), retaining 100 trees per replicate. The characters were analysed using equal weigth of characters and implied weights (Farris, 1988; Goloboff, 1993, 1995; Ponssa, 2008). The more homoplastic characters (the more homoplastic, the less fit) are lower weight characters. Analyses were conducted each with constant of concavity (*k*) set to a different integer value from 1 to 6, where 1 is weighted most severely against homoplasious characters. The support of the clades was calculated by symmetric resampling (1000 replicates, with 10 addition sequences, saving up to 10 trees each) expressed as absolute frequencies (Goloboff et al., 2003), absolute and relative Bremer support (Goloboff & Farris, 2001).

Parsimony analysis using TNT was run on DPII and DPIII with *Euconulus* as outgroup since the software only works with one-taxon outgroup.

Bayesian inference (BI) analysis was run on DPIII (since it was the dataset on which more results were found by the other analyses) using MrBayes (version 3.1, Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Mkv models for discrete morphological data were applied to our dataset (Lewis, 2001). Two analyses were run: the first assuming equal rates of change among characters; the second with four rate categories of the gamma distribution parameter, allowing different character change rates across characters. Bayes factors (following Kass & Raftery, 1995; Nylander et al., 2004) were used to compare these two models and find model fitting evolution of the data best. Differences in harmonic means of log likelihoods of the two models multiplied by two were calculated. One model was preferred over the other for values > 10 (Nylander et al., 2004; Wiens, 2005). The default value of four Markov chains was used (one cold and three heated) and each chain was started from a random tree. The "temperature" parameter was set at 0.2. Monte Carlo Markov Chain length was 2,000,000 generations and trees were sampled every 100 generations. To establish whether the Markov chains had reached a steady state, we plotted the −ln likelihood scores of sampled trees against generation time. Log-likelihood scores were plotted to determine the number of trees to be discarded (i.e., to determine the length of the burn-in period). Only trees sampled after this burn-in period were used to construct a 50% majority rule tree.

RESULTS AND DISCUSSION

Vitrinid Phylogeny

Phylogeny analysis generally had low resolution although AP was better than the other methods (AP found 11 supported clades, MP 11 and BI 8; Table 3). AP also recovered all supported clades found by MP except four (clades 6, 9, 12 and 16) and by BI except two (clades 5 and 13).

Using Paup*, MP only revealed slight differences between the three datasets (DPI, DPII, DPIII) and almost never between the three analyses (1, 2 and 3). The analyses which produced more results were those on DPII and DPIII (8 and 9 supported clades respectively; DPII (3): length L = 486; consistency index CI = 0.273; retention index RI = 0.345; rescaled consistency index RCI = 0.094; DPIII (3): length L = 88; consistency index CI = 0.282; retention index RI = 0.287; rescaled consistency index RCI = 0.081).

Using TNT, AP revealed some differences between the two datasets (DPII, DPIII) (Table 3). Moreover, since the analyses with implied weigth showed the same or more results than those with equal weight, only the results under implied weigth are showed (Figs. 14, 15). For DPII (7 supported clades; Table 3), AP found 27 most parsimonious trees (tree length = 100 steps, CI = 38, RI = 56 for K = 3; Fig. 14) showing more basal groups, even if with low support, and two clades where *Vitrea crystallina* is sister group of the two *Vitrinobrachium* species and *Troglaegopis mosorensis* is grouped with *Semilimacella bonelli* and *Vitrina pellucida*. For DPIII (8 supported clades; Table 3), AP found 49 most parsimonious trees (tree length = 103 steps, CI = 35, RI = 44 for K = 3; Fig. 15).

As for BI analyses, the total harmonic means were -349.62 (equal rates of change among characters) and -346.87 (four rate categories of the gamma distribution parameter), and the resulting difference in harmonic means of log likelihoods of the two models multiplied by two was 5.5. Thus the gamma shape parameter is not preferred on the model, which assumes equal rates of change among characters. BI analysis recovered most of the clades found by MP plus two (*Arabivitrina arabica*, *A. jansseni*; and *Semilimacella bonelli*, *Semilimacella cephalonica*; Table 3).

Phylogeny analysis of DPI and DPII did not reveal monophyly of vitrinids, as MP and AP included some taxa of the outgroup in the ingroup. MP and AP analysis on DPII only found a basal, variably supported clade consisting of all vitrinids plus *Troglaegopis mosorensis* and *Vitrea crystallina* (MP: 55–60%; AP: 62% symmetric resampling, 0.23/38 Bremer absolute and relative supports). Only when the outgroup was reduced to two taxa (removing *Deroceras laeve*, *Tandonia budapestensis*, *Troglaegopis mosorensis* and *Vitrea crystallina*, DPIII), did the vitrinids prove to be a monophyletic group (MP: 88%; AP: 89% symmetric resampling, 0.61/62 absolute and relative Bremer supports) (Figs. 14, 15).

Apart from the basal inclusive groups, MP found nine monophyletic groups, none strongly supported except one (*Vitrinobrachium baccettii* - *V. breve*). All MP-supported monophyletic groups except three included only two terminal taxa; the three included the *Azorivitrina* species

TABLE 3. List of selected clades (clades with ≥ 50% bootstrap support for MP; ≥ 50% symmetric resampling support for AP with implied weigth and/or ≥ 7 and ≥ 50% absolute and relative Bremer support for AP with implied weigth) and their synapomorphies. MP: parsimony analyses by PAUP, AP: parsimony analyses using implied weights by TNT, BI: Bayesian inference by MRBAYES (equal weight), 1–3: analyses 1–3 (if not specified, clade appears in all analyses). When a clade appears in more than one analysis, the synapomorphies are in bold if they support the clade in all the analyses. *: only relative Bremer support.

No	Clade	MP	MP synapomorphies	AP	AP synapomorphies	BI
1	Vitrinids + *Oxychilus cellarius*, *Troglaegopis mosorensis*, *Vitrea crystallina*			DPII	**no common synapomorphies**	
2	Vitrinids + *Oxychilus cellarius*			DPIII	**no common synapomorphies**	
3	Vitrinids + *Troglaegopis mosorensis*, *Vitrea crystallina*	DPII	**1(1) 5(1) 7(1) 8(1) 13(2) 14(1) 17(1) 25(2)**	DPII	**8(1) 17(1)**	
4	Vitrinids	DPIII	**1(1) 5(1) 7(1) 8(1) 12(1) 13(2) 14(1) 17(1) 25(2)**	DPIII	**1(1) 8(1) 13(2) 17(1)**	DPIII
5	*Arabivitrina arabica*, *Arabivitrina jansseni*					DPIII
6	*Azorivitrina brevispira*, *Azorivitrina finitima*, *Azorivitrina laxata*	DPI (3), DPII (3), DPIII (3)	**12(1)** 14(1) **21(1)**			
7	*Canarivitrina dianae*, *Canarivitrina taburientensis*	DPI, DPII, DPIII	12(1) 14(1) **17(3) 19(1)**	DPII, DPIII	**19(1)**	DPIII
8	*Guerrina christinae*, *Guerrina cuticula*	DPI, DPII, DPIII	**1(0) 6(1)** 12(1) 14(1) **17(2) 18(1)**	DPII, DPIII	**1(0)**	DPIII
9	*Hessemilimax kotulae*, *Semilimax carinthiacus*, *Semilimax pyrenaicus*, *Semilimax semilimax*	DPII (2)	**5(2) 7(0) 12(1) 14(0) 15(0) 22(2)**			
10	*Madeirovitrina marcida*, *Madeirovitrina nitida*	DPI, DPII, DPIII	12(1) 14(1) **17(2) 18(1) 20(1)**	DPII, DPIII	**20(1)**	DPIII
11	*Oligolimax annularis*, *Oligolimax musignani*	DPIII	**1(0) 6(1) 11(1) 14(1) 25(1)**	DPII*	**1(0)**	DPIII
12	*Oligolimax annularis*, *Oligolimax musignani*, *Sardovitrina polloneriana*, *Semilimacella bonelli*, *Semilimacella cephalonica*, *Vitrina pellucida*	DPIII (3)	**11(1)**			
13	*Semilimacella bonelli*, *Semilimacella cephalonica*					DPIII
14	*Semilimacella bonelli*, *Semilimacella cephalonica*, *Vitrina pellucida*			DPIII	**5(2) 7(0)**	
15	*Semilimacella bonelli*, *Vitrina pellucida*			DPII*	**3(1)**	
16	*Semilimax pyrenaicus*, *Semilimax semilimax*	DPI (2), DPII (2, 3), DPIII (2, 3)	5(2) 7(0) **9(2)** 15(0) 22(2)			
17	*Vitrinobrachium baccettii*, *Vitrinobrachium breve*	DPI, DPII, DPIII	**4(1) 5(2) 7(0) 10(1)** 12(0) 14(0) 15(1) **23(0) 24(4)**	DPII, DPIII	**4(1)** 5(2) 10(1) 25(2)	DPIII

(1), *Hessemilimax kotulae* with the species of *Semilimax* (2), and species of *Oligolimax*, *Sardovitrina*, *Semilimacella* and *Vitrina* (3), respectively.

AP analysis produced well supported monophyletic groups (Table 3). Although most of the monophyletic groups consisted of only two terminal taxa, some were more inclusive (Figs. 14, 15).

Like MP, BI found a basal largely unresolved group and a few monophyletic groups, all consisting of two terminal taxa.

Vitrinid Systematics

Phylogenetic analysis did not support monophyly of most genus-group taxa or the monophyletic groups found by Hausdorf (1995, 2002) and Alonso et al. (2000), or the subfamilies and tribes established by Schileyko (1986, 2003), or the family Vitrinidae if the outgroup was conceived as consisting of a large selection of taxa of the larger monophyletic group to which vitrinids belongs, the limacoideans.

Regarding the genera, we found good support for monophyly of *Canarivitrina*, *Guerrina*, *Oligolimax* and *Vitrinobrachium* and sufficient support for monophyly of *Azorivitrina*. Notably three of these genera (*Canarivitrina*, *Guerrina* and *Azorivitrina*) are represented by insular endemics characterized by exclusive synapomorphies of the penial complex. On the contrary, we did not find any support for monophyly of *Eucobresia*, *Insulivitrina* and *Phenacolimax*, or for *Plutonia sensu* Alonso et al. (2000).

The most resolved group found was a clade including species of *Oligolimax*, *Sardovitrina*, *Semilimacella* and *Vitrina*, but with low support (MP: 50%; AP (DPIII): 9% symmetric resamplig, 0.15/40 absolute and relative Bremer supports; Figs. 14, 15, Table 3). This clade was supported by exclusive disposition of the penial retractor above the right ommatophore retractor. A sister-group relationship between *Oligolimax* and *Sardovitrina* was already suggested by Manganelli & Giusti (2005) when describing the latter genus. This clade includes taxa with glandula amatoria (*Oligolimax* and *Sardovitrina*), diverticular stimulator (*Semilimacella*) or lacking stimulatory structures (*Vitrina*). Relationships between *Semilimacella* and *Vitrina* were found by Hausdorf (2002); however those between the two species of *Semilimacella* and *Vitrina pellucida* are controversial: we found more support for the group *Semilimacella bonelli* – *Vitrina pellucida* than for that consisting of the two *Semilimacella* species (Table 3).

Another inclusive monophyletic group was represented by *Calidivitrina* cf. *oleosa* and species of *Guerrina* and *Madeirovitrina*, but it had low support (AP (DPII): 13% symmetric resampling, 0.07/36 absolute and relative Bremer supports; AP (DPIII): 16% symmetric resampling, 0.04/29 absolute and relative Bremer supports) (Figs. 14, 15). The group is characterized by two non exclusive synapomorphies (17(2) and 18(1)). It may be biased by the fact that it was only possible to examine two specimens (one adult already dissected and one juvenile) of a single species of *Calidivitrina*.

Our study failed to produce a definitive generic classification for the vitrinids, however it showed that *Plutonia* cannot be accepted in the sense of Alonso et al. (2000) or Schileyko (2003). We therefore prefer to rank the eighteen genus-group taxa considered in our survey as distinct genera, awaiting further research. We are perfectly aware that many of them may be paraphyletic or polyphyletic, but there is no alternative for the present. In the remarks to each genus we discuss the main problems related with its systematic status and relationships. Vitrinid phylogeny and systematics require a different approach because morphological characters alone are not able to generate a realistic phylogeny and systematics.

SYSTEMATIC REVISIONS

This section includes a concise survey of all the vitrinid genera, preceded by a redescription of the family. The genera are listed alphabetically in three distinct groups according to stimulator structure: vitrinids with vaginal stimulator (glandula amatoria) (1); vitrinids with diverticular stimulator (atrial/atrial-vaginal/vaginal or penial diverticular stimulator) (2); vitrinids without vaginal or diverticular stimulator (3). This approach was used to enable easy comparisons between taxa with similar distal genitalia structures and is not intended to have any systematic or phylogenetic value. For each taxon a short diagnosis, a description of the type species and some remarks are given.

VITRINIDAE Fitzinger, 1833

Type Genus: *Vitrina* Draparnaud, 1801.

Diagnosis

Semislug-like pulmonates with thin, glossy, translucent, ear-like dorsal shells partially

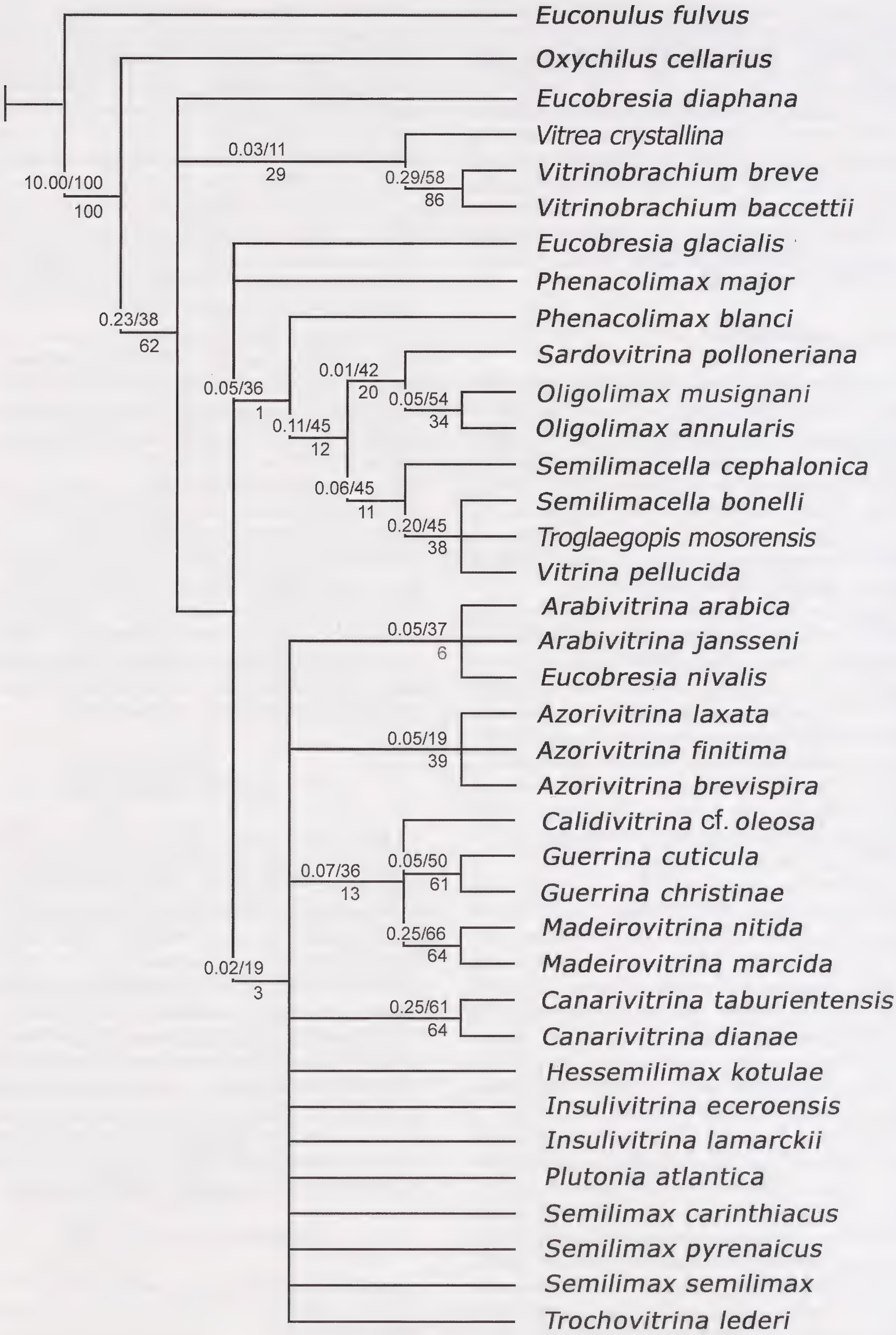


FIG. 14. Strict consensus of the 27 most parsimonious trees obtained under implied weights with concavity K = 3 on DPII (AP analysis). Values at nodes are absolute and relative Bremer support (above) and symmetric resampling (below).

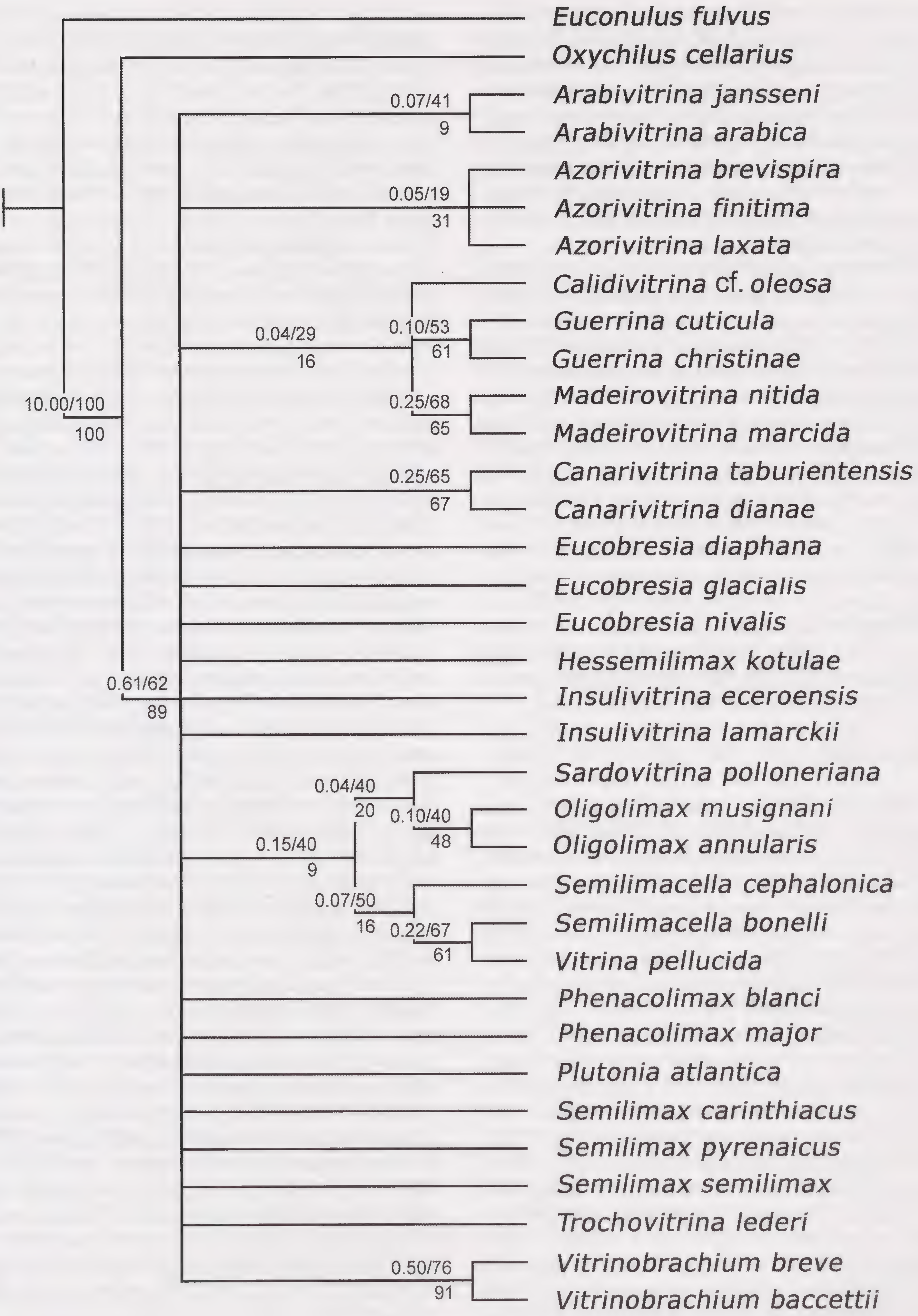


FIG. 15. Strict consensus of the 49 most parsimonious trees obtained under implied weights with concavity K = 3 on DPIII (AP analysis). Values at nodes are absolute and relative Bremer support (above) and symmetric resampling (below).

covered by large to very large anterior dorsal mantle shield and spatulate right shell lobe (though some derived taxa reverted to snail-like or acquired slug-like habitus); distal genitalia without epiphallus, with distinctive accessory stimulator structures consisting of vaginal glandula amatoria or distinct blind diverticulum associated with atrium or vagina or penial complex (but some derived taxa without accessory stimulator structures).

Within the geographical range of the family, no other similar semislugs exist. The western Palaearctic zonitids *Carpathica*, *Daudebardia* and *Libania* and the testacellid *Testacella* have a posterior shell and lack the mantle shield and a spatulate right shell lobe, while the parmacellids *Parmacella* and *Candaharia* have a dorsal shell consisting of a normal coiled protoconch and a nail-like teleoconch entirely covered by mantle shield (for zonitids: Riedel, 1980; for testacellids: Quick, 1960; for parmacellids: Solem, 1979). The Nearctic zonitid *Vitrinizonites* has a dorsal shell but lacks the mantle shield and spatulate right shell lobe (Pilsbry, 1946). The Afrotropical urocyclids *Gymnarion*, *Africarion*, etc. have a large dorsal shell partly covered by mantle shield, but a truncated tail with caudal fossa and horn (Schileyko, 2002).

Description

Body snail-like (species of *Guerrina*, *Oligolimax* and *Trochovitrina*), semislug-like (most vitrinids) or slug-like (only *Plutonia atlantica*). Snail-like vitrinids have shell large enough to withdraw body into it completely; on the contrary, semislug-like vitrinids have shell reduced so that they cannot withdraw body into it completely. Slug-like *Plutonia* has an internal limacella-like shell.

Mantle edge usually with one or two latero-posterior shell lobes, one more or less triangular right body lobe and one left – dorsal body lobe extending anteriorly to give rise to large to very large dorsal mantle shield (shell lobes absent and mantle shield very small in *Guerrina*, *Oligolimax* and *Trochovitrina*). Right shell lobe always more developed than left shell lobe (when present), more or less spatulate and covering a more or less wide portion of dorsal surface of shell; left shell lobe usually consisting of narrow strip or absent (in re-descriptions of genera, only the right shell lobe is considered, because available images of living specimens only depict their right side – cf. Kerney & Cameron, 1979; Bogon, 1990; Falkner, 1990, 1992 – and in the preserved material shape and size of shell lobes are modified due to fixation).

Foot aulacopod and sole tripartite with distinct longitudinal furrows meeting a short distance from tail tip. Posterior part of foot, below shell, with dorsal flat triangular area bordered by two raised crests which meet at about half tail length; raised keel originates at this point and ends at tail tip.

Jaw oxygnathous except in *Plutonia*, which has very arched jaw without central outgrowth.

Radula dichoglossan except in *Plutonia* where it is beloglossan (Jungbluth et al., 1985); structure of marginal teeth variable with mono- or pluricuspid teeth inside species of same genus.

Shell very thin and fragile, consisting of few whorls (never more than four) and ranging in shape from globular-conical (*Oligolimax*) to globular-depressed (*Vitrina*), conical-depressed (*Guerrina*, *Trochovitrina*) or depressed (*Arabivitrina*, *Eucobresia*, etc.). Vitrinid shells differ in shape of last whorl and width of aperture: last whorl expanded and aperture moderately wide in typical vitriniform and trochiform shells (they differ in periphery, which is rounded in typical vitriniform shells, see *Vitrina*, etc., and angled or keeled in trochiform shells, see *Guerrina* and *Trochovitrina*); last whorl well expanded and aperture wide in slightly dilated vitriniform shells (*Arabivitrina*, *Canarivitrina*, etc.); last whorl extremely expanded and aperture very wide in very dilated vitriniform shells (*Semilimax*, *Vitrinobrachium*, etc.). Columellar and basal margins of aperture with variably wide membranous border ("periostracal fringe"; absent in *Guerrina* and *Trochovitrina*). In some species (*Eucobresia diaphana*, *Hessemilimax kotulae*, etc.), columellar margin more or less cut-away so that internal winding of spire is visible. Umbilicus closed or punctiform; when columellar margin cut-away umbilical area is open. Protoconch usually smooth, sometimes more or less evidently ribbed; in both cases mineralized part, below periostracum, more or less evidently and variably pitted (five different types recognized by Ibáñez et al., 1987); sometimes pits ("puncta") few and sparse, but usually numerous and arranged in many spiral rows. Teleoconch usually smooth, sometimes with fine, closely and regularly spaced radial riblets (*Guerrina*, some *Oligolimax* and *Trochovitrina*).

Proximal genitalia (those including parts close to the gonad: first hermaphrodite duct, talon or seminal receptacle - fertilization pouch complex, albumen gland, second hermaphrodite duct or ovispermiduct) do not show significant variation between the various taxa, whereas distal genitalia have very complex and diverse structure.

Female distal genitalia include: free oviduct, bursa copulatrix and its duct and vagina. Free oviduct variably long and wide. Bursa copulatrix ("bursa of receptaculum seminis", Forcart, 1959; "gametolytic gland", Valido et al., 1993; "spermatheca", Hubendick, 1953; Forcart, 1959; Schileyko, 2003) usually rather small (oval, roundish or pyriform) and with variably long duct, sometimes initially flared. Vagina absent in *Vitrinobrachium*, very short/short in *Calidivitrina*, *Eucobresia*, *Hessemilimax*, *Semilimacella*, *Semilimax* and *Vitrina* and long in vitrinids with glandula amatoria. In some species of *Semilimacella* and *Vitrina*, vagina and initial part of duct of bursa copulatrix with external glandular layer imitating vaginal gland of zonitids. In *Hessemilimax*, *Semilimacella*, *Semilimax* and *Vitrina*, vagina lacks any internal structure. In *Calidivitrina* and type species of *Eucobresia* there is an internal proximal pad; in another alleged *Eucobresia* species (*E. nivalis*) there is a small conical papilla-like structure similar to that of a typical glandula amatoria (detailed description is given under remarks to *Eucobresia*). In the other vitrinids, vagina has distinct proximal and distal portions; proximal corresponding to vaginal stimulator, so called "glandula amatoria" ("stimulator", Mordan & Martins, 2001; "stimulator portion of vagina", Hausdorf, 1995; Alonso et al., 2000; "vaginal gland", Hubendick, 1953; Mordan & Martins, 2001; "vaginal stimulator", Muratov, 1999). Glandula amatoria is sort of wide cylinder with muscular walls covered externally and internally by glandular tissue layer; external glandular layer may partially or completely cover muscular wall and may extend to distal free oviduct and beginning of bursa copulatrix duct; its secretion is conveyed into vaginal lumen through very thin channels in muscular wall; internal glandular layer is always complete and defines narrow lumen. Distally, glandula amatoria has variably developed conical papilla ("spout", Ibáñez et al., 2001; "stimulatory papilla", Mordan & Martins, 2001; "vaginal papilla", Forcart, 1957), open at tip, protruding into distal vagina. Final part of proximal vagina is usually invaginated inside distal vagina; externally, level with initial part of invaginated portion, walls of distal vagina are connected to those of glandula amatoria by thin stripes of muscular tissue which presumably prevent evagination. *Trochovitrina* apparently lacks papilla of glandula amatoria. Distal vagina has very thin, subtransparent walls, sometimes with sparse traces of glandular tissue; internal surface of distal vagina with regularly or irregularly arranged pleats and sometimes longitudinal pilasters (*Canarivitrina*, *Oligolimax*) or laminar crests (*Plutonia*).

Male distal genitalia include vas deferens and penial complex (epiphallus absent). Vas deferens of variable length (long in *Hessemilimax*, *Phenacolimax*, *Semilimacella*, *Semilimax*, *Vitrina* and *Vitrinobrachium*; short to medium in the other genera). It may enter penial complex apically/subapically (*Plutonia* and *Sardovitrina*) or medially to distally, thus distinguishing short to long flagellum and penis proper (*Calidivitrina*, *Canarivitrina*, *Guerrina*, *Madeirovitrina* and *Trochovitrina*). Other times vas deferens contacts penial complex about medially, then traverses penial sheath (if present), running along or inside thickness of penial gland and entering penial complex subapically near insertion of penial retractor (*Arabivitrina*, *Eucobresia*, *Hessemilimax*, *Insulivitrina*, *Oligolimax*, *Phenacolimax*, *Vitrina* and *Vitrinobrachium*).

Penial complex ("penis", most authors) is very variable in shape and size: very small (e.g., *Oligolimax* and *Sardovitrina*) to large (*Canarivitrina*, *Eucobresia*, etc.), finger-like (*Canarivitrina*, *Vitrina*, etc.), club-like (*Calidivitrina*, *Eucobresia*, etc.), nearly bilobate (*Arabivitrina* and *Plutonia*) or more or less globular (*Sardovitrina*, *Vitrinobrachium*, etc.) and may have or not have a penial gland and a penial sheath. Penial gland ("apical gland", Hausdorf, 1995, 2002) is an external layer of glandular tissue covering most of penial complex (*Eucobresia*, *Phenacolimax*, etc.), or most of proximal penial complex (*Madeirovitrina*, *Oligolimax*, etc.), or part of side of penial complex facing vagina (*Arabivitrina*, *Insulivitrina*, etc.), or forming sparse glandular covering (*Sardovitrina*). Penial sheath ("penial tunica", Hausdorf, 1995, 2002) is a thin short to long sac present in *Eucobresia*, *Hessemilimax*, *Phenacolimax*, *Semilimacella*, *Semilimax*, *Vitrina*, *Vitrinobrachium* and in some species of Macaronesian vitrinids (*Azorivitrina finitima*, *Insulivitrina blauneri* and *I. lamarckii*). It may arise from distal constriction and envelope most of penial complex or from a mid constriction and envelope proximal penial complex only. It is basally traversed by vas deferens on one side (in oxychiline zonitids it is traversed apically), apically open and often wrinkled.

Penial retractor muscle arising from diaphragm (all genera except *Vitrinobrachium*) or columellar muscle (*Vitrinobrachium*) and ending on penial complex apically or subapically. Penial retractor modified in *Plutonia atlantica* being subdivided into three branches, none of which reaches penial complex: first reaches bursa copulatrix and its duct, second reaches free oviduct and third reaches vas deferens (sometimes thin muscular branches connect distal vas deferens and penial complex). Muscle bundles connecting free oviduct to duct of bursa copulatrix also present in *Madeirovitrina marcida* and *M. nitida* although these species have normal penial retractor. Finally, penial rectractor absent in two species of *Semilimax* (*S. semilimax* and *S. pyrenaicus*) and absent or vestigial in one species of *Azorivitrina* (*A. finitima*).

Internal stuctures of penial complex variable in shape, size and number: they may consist of main pilaster only (*Calidivitrina*, *Semilimacella*, *Semilimax*, *Trochovitrina* and *Vitrina*), main and accessory pilasters (*Arabivitrina*, *Guerrina*, *Madeirovitrina*, *Oligolimax*, *Phenacolimax* and *Plutonia*), two distinctive pilasters possibly homologous with main and accessory pilasters (*Eucobresia* and *Insulivitrina*), branched main pilaster (*Hessemilimax*) or extremely distinctive structures (*Canarivitrina*, *Sardovitrina* and *Vitrinobrachium*). Main pilaster usually consists of large proximal "glandular roll" (Hausdorf, 1995, in *Oligolimax*), sometimes distally lamellate and sometimes with distal smooth muscular pleat, ending in or before genital atrium. Glandular roll is a sort of elongated knoll, located inside innermost penial complex, usually in correspondence with external penial gland (especially evident in those species in which penial gland forms band on one side of penial complex). This structure has been named: "Drüsenwülste der Penis" (Forcart, 1959, in *Oligolimax*), "glandular pad" (Mordan & Martins, 2001, in Azorean "*Plutonia*"), "penial glandular torus" (Forcart, 1957, in *Arabivitrina*), "penis gland" (Hubendick, 1953, in *Arabivitrina* and *Calidivitrina*) or "torus" (Alonso et al., 2000, in *Canarivitrina*). Apart from *Sardovitrina* and *Vitrinobrachium*, all the other genera have usual or modified glandular roll. In *Arabivitrina*, *Calidivitrina*, *Guerrina* and *Madeirovitrina*, distal portion of glandular roll is lamellate; in *Canarivitrina*, *Eucobresia*, *Insulivitrina*, *Oligolimax* and *Phenacolimax* lamellate portion is not evident, but distal portion is more or less pleated; in *Hessemilimax*, *Plutonia*, *Semilimacella*, *Semilimax*, *Trochovitrina* and *Vitrina* no lamellate or pleated distal portion is evident. Glandular roll may stop abruptly near penis and open into genital atrium (*Plutonia*, *Semilimacella*, etc.) or continue uninterrupted into genital atrium as muscular pleat, having more or less evidently pleated or wrinkled surface (*Guerrina*, *Madeirovitrina*, etc.).

Accessory pilaster consists of longitudinal, superficially pleated or wrinkled structure arising side by side or from one side of glandular roll, running parallel to main pilaster, then continuing forwards, ending before or inside genital atrium. Peculiar pilasters are observed in *Canarivitrina* and *Madeirovitrina*. In the former, accessory pilaster consists of wrinkled laminar structure (which suggested name "laminar crest" or "velum"; Alonso et al., 2000). In the latter (at least in species here re-examined), accessory pilaster arises on one side of glandular roll and ends near gonopore; remarkably its medial portion is detached from genital walls as free cordon. Other structures are situated close to where penis opens into genital atrium: crescent-like crest in *Semilimacella bonelli*; tongue-like structure in *Phenacolimax major*; tongue-like structure fused with tip of main pilaster in *Insulivitrina lamarckii*.

Opening of vas deferens into penial lumen is located on glandular roll (*Madeirovitrina*, *Oligolimax*, *Phenacolimax*, *Plutonia*, *Trochovitrina*), or at tip of cylindrical papilla (*Canarivitrina* and *Sardovitrina*) or in flat structure divided into two semicircular tiles (*Vitrinobrachium*). In other cases, opening of vas deferens is not visible, but probably situated level with glandular roll.

In all species examined, genital nerve arises from right pedal ganglion, extends towards distal genitalia and ends with distinct branches on walls of distal penial complex and distal vagina.

In *Hessemilimax*, *Semilimacella*, *Semilimax* and *Vitrinobrachium*, a diverticular stimulator, consisting of more or less elongated blind sac with apical portion covered by spongy glandular tissue, is associated with the distal genitalia ("accessory organ", Forcart, 1956, 1957; "appendix", Forcart, 1956, 1957; "atrial diverticulum", Alonso et al., 2000; "Begattungsarm", Künkel, 1929, 1933; "brachium copulatorium", Forcart, 1956, 1957; "copulatory gland", Hubendick, 1953; "glande femelle", Germain, 1930; "Liebesdrüse", Hesse, 1923; "penial appendage", Kerney & Cameron, 1979; "penial appendix", Kerney & Cameron, 1979; "Pfeilsack", Wagner, 1915; "sarcobelum", Schileyko, 2003; "stimulator", Hausdorf, 1998, 2002; "vaginal sarcobellum", Muratov, 1999).

In *Hessemilimax*, *Semilimacella* and *Semilimax*, a diverticular stimulator is inserted, opposite where penial complex enters one side of genital atrium (atrial stimulator) or between vagina and genital atrium (atrial-vaginal stimulator) or on one side of distal vagina (vaginal stimulator). To the contrary, in *Vitrinobrachium* it is inserted in distal penial complex and may be termed "penial stimulator". Stimulator of *Hessemilimax* and *Semilimax* has structure very similar to that of glandula amatoria, but differs in that its internal cavity is not covered by layer of glandular tissue. Detailed description of these structures is given under the relevant genera.

Genital atrium is usually long or very long, the most remarkable exception being *Phenacolimax major* which has a very short genital atrium. In most cases, the vaginal side or both sides of genital atrium have many variably robust muscular bundles connecting them to body wall.

Relationships between right ommatophore retractor, penial retractor and distal genitalia are different in various taxa and sometimes age-dependent (Figs. 3–11). In juveniles and adults of *Oligolimax*, *Sardovitrina*, *Semilimacella* and *Vitrina* penial retractor is long and passes above the right ommatophore retractor, leaving it free of penial complex and vagina. In juveniles and adults of *Semilimax carinthiacus*, *Hessemilimax kotulae, Vitrinobrachium* and all Macaronesian vitrinids (except *Plutonia*) and in juveniles of *Arabivitrina*, *Eucobresia* and *Phenacolimax*, penial retractor is long and passes below right ommatophore and in front of right optic nerve; distal genitalia lie right of right ommatophore retractor which therefore appears free of penial complex and vagina (actually it is free only because the genitalia lie right of the right ommatophore retractor). In adults of *Arabivitrina*, *Eucobresia* and *Phenacolimax*, penial retractor is short and passes below right ommatophore retractor and in front of right optic nerve; right ommatophore retractor is consequently shifted to right and compelled to lie more or less between the penial complex and vagina.

Mating face-to-face, simultaneously reciprocal. Mating has only been described in detail in two species (*Semilimax semilimax* and *Vitrinobrachium breve*) which copulate keeping partner still by means of suckers or sucker-like structures of diverticular stimulator. In *V. breve*, sperm transfer is external (everted penial complex not inserted in vagina or duct of bursa copulatrix), whereas in *S. semilimax* it is internal (everted penial complex inserted in vagina or duct of bursa copulatrix) (Künkel, 1929, 1933). According to Hausdorf (2002), the stimulator is not used to keep partner still in *Eucobresia* and *Phenacolimax* while sperm transfer is internal in *Eucobresia* and *Vitrina* and external in *Phenacolimax* and *Plutonia* (but see remarks to these genera on *Eucobresia* and *Plutonia sensu* Hausdorf, 2002).

Vitrinids with Vaginal Stimulator (glandula amatoria)

The vitrinids with glandula amatoria include most taxa of the genus group described in the vitrinids. They are characterized by the vaginal stimulator; as it is a unique and complex structure, it presumably only appeared once in the evolution of the group. MP analysis found that the glandula amatoria is a synapomorphy of the family (Table 3).

Arabivitrina Thiele, 1931

Type Species: *Vitrina arabica* Thiele, 1910, by monotypy.

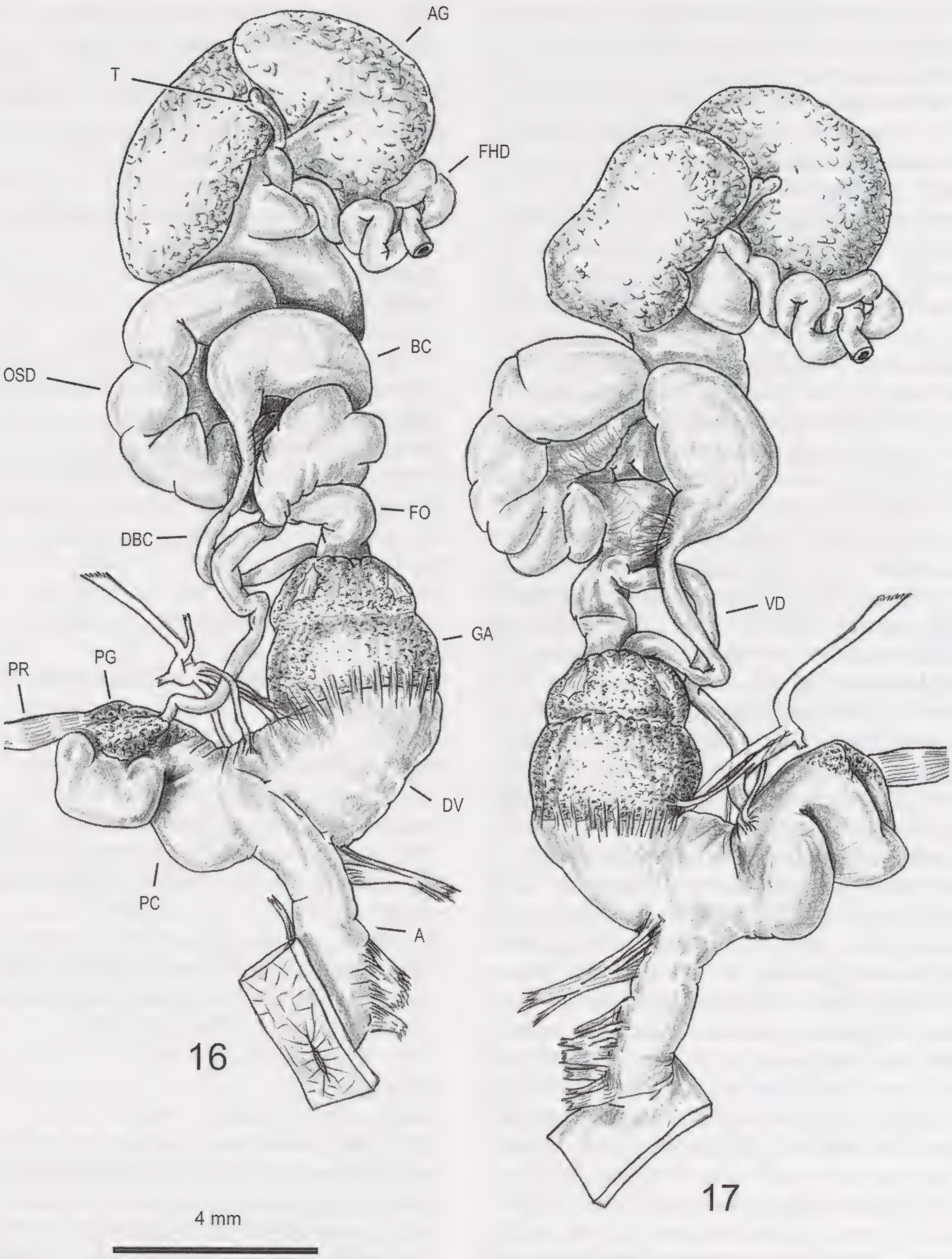
Material Examined

Arabivitrina arabica (Thiele, 1910) – Saudi Arabia: Rayah escarpment ('Asīr), P. Symens & M. Werner leg. 29.1.1994 (3 spirit specimens, SMF 311595)

Arabivitrina jansseni Neubert, 1998 – Saudi Arabia: 15 km S of Bani Sa'ad Sof Ta'if ('Asīr), R. Janssen & E. Neubert leg. 2.6.1995 (1 spirit specimen, SMF 311607).

Diagnosis

Semislug-like vitrinids characterized by short penial retractor muscle arising from diaphragm compelling penial complex below right ommatophore and in front of right optic nerve and ending on penial complex subapically (but juveniles with long penial retractor muscle running in front of right optic nerve below right ommatophore retractor); stimulator consisting of glandula amatoria with complete external glandular covering; penial complex with penial gland and without penial sheath; vas deferens contacting penial complex about medially, running inside its wall and entering it subapically; internal structures of penial complex comprising main and accessory pilasters; main pilaster consisting of large, distally lamellate, proximal glandular roll.



FIGS. 16, 17. Distal genitalia of a specimen of *Arabivitrina arabica* (Thiele, 1910) from Rayah escarpment (ʻAsīr, Saudi Arabia), P. Symens & M. Werner leg. 29.1.1994.

Description of Type Species

Shell: vitriniform slightly dilated, glossy, thin and fragile, depressed, with 2.5–3.0 whorls; last whorl well expanded; aperture wide with basal margin bordered by narrow periostracal fringe; columellar margin normal; umbilicus closed; protoconch not prominent, smooth, with many regular spiral rows of very small pits; teleoconch with blunt radial ribs (Neubert, 1998: figs. 88–90).

Body: Hesse (1923: 136) described shell lobes but not dimensions. Neubert (1998: 388, fig.

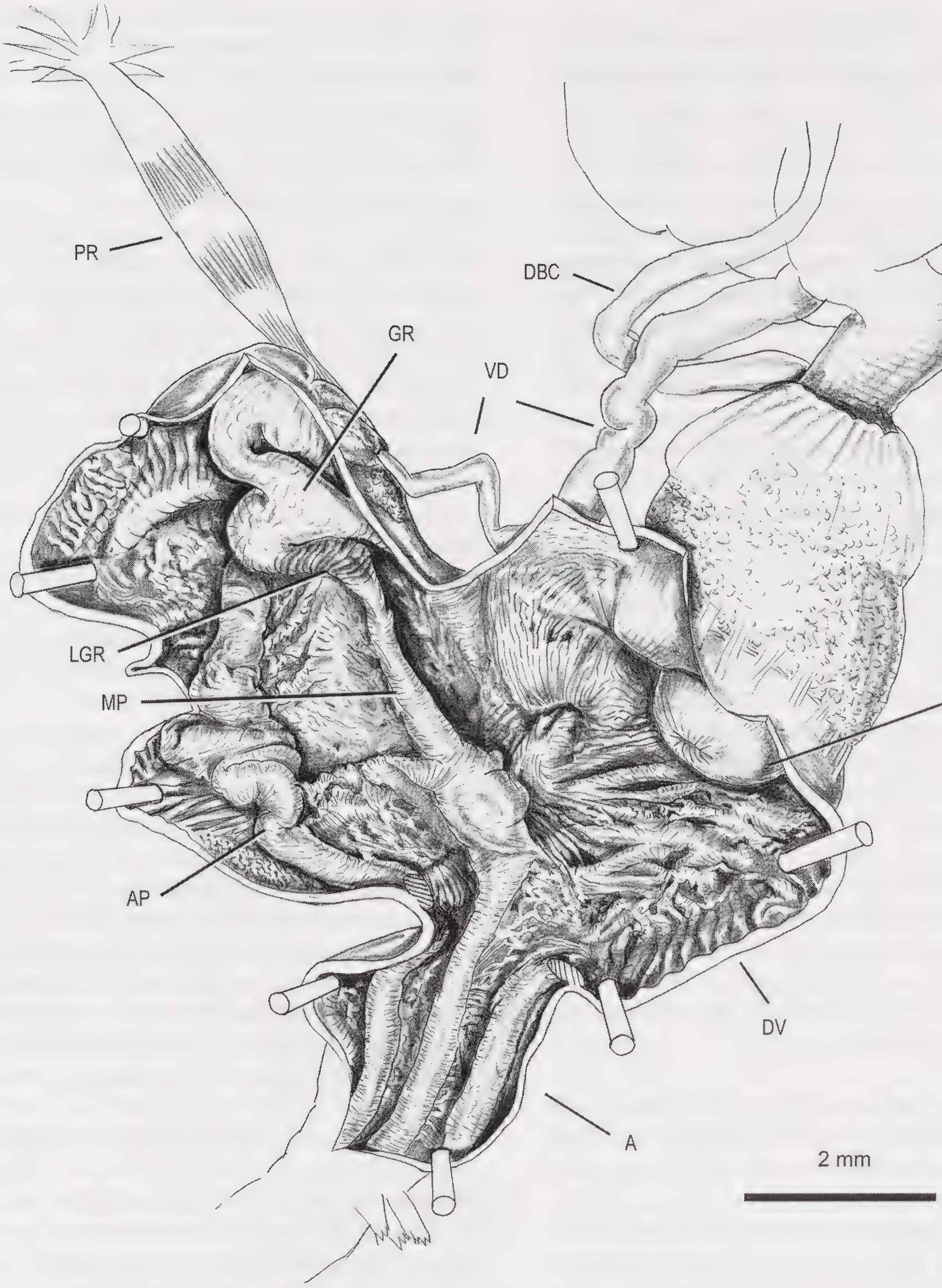


FIG. 18. Internal structure of distal genitalia of a specimen of *Arabivitrina arabica* (Thiele, 1910) from Rayah escarpment (ʻAsīr, Saudi Arabia), P. Symens & M. Werner leg. 29.1.1994.

101) stated that another *Arabivitrina* species, *A. jansseni*, cannot withdraw body completely into shell and that right shell lobe is small.

Radula: dichoglossan. Hesse (1923: 137) stated that marginal teeth are bicuspid.

Female Distal Genitalia (Figs. 16–18): free oviduct short and wide. Bursa copulatrix medium in size and oval to shoe-like in shape, with medium to long, very slender duct, initially not flared. Vagina long, with large bulbous glandula amatoria constituting half its length. Glandula amatoria with very thick muscular wall, almost completely covered by external glandular layer; papilla of glandula amatoria very short. Internal surface of distal vagina with thin pleats irregularly arranged.

Male Distal Genitalia (Figs. 16–18): penial complex small and nearly bilobate, with penial gland and without penial sheath. Penial gland covering side of proximal penial complex facing vagina. Penial retractor arising from diaphragm, short, inserted subapically. Vas deferens medium in length, contacting penial complex about medially, then running inside thickness of penial gland and entering penial complex subapically near insertion of penial retractor. Internal structures of penial complex comprising main and accessory pilasters. Main pilaster consisting of large proximal glandular roll ("penial gland"; Neubert, 1998: fig. 97), initially slender, sometimes twisted on itself, then wider and distally lamellate ("lamellate pilaster"; Neubert, 1998: fig. 97) and medial–distal superficially wrinkled slender muscular pleat ("main pilaster"; Neubert, 1998: fig. 97), ending in genital atrium. Accessory pilaster ("longitudinal pilaster"; Neubert, 1998: 387) slender, arising near lamellate portion of glandular roll and ending in genital atrium, sometimes branching into two. Vas deferens opening not visible, probably on side of glandular roll. Internal surface with low irregularly arranged pleats and sparse spongy tissue with crypts.

Genital Atrium (Figs. 16–18): long and cylindrical, with one side connected to body wall by robust muscular bands. Internal structures consisting of short pilaster and distal portion of main and accessory pilasters. Internal surface as in penial complex.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: age-dependent (Figs. 3, 6). Juveniles (Fig. 3) with long slender penial retractor passing below right ommatophore and in front of right optic nerve; distal genitalia lying right of right ommatophore retractor which therefore appears free of penial complex and vagina. Adults (Fig. 6) with penial retractor short so that entire penial complex is below right ommatophore and in front of right optic nerve; right ommatophore is consequently shifted to right and compelled to lie between penial complex and vagina.

Mating: no data available.

Remarks

Arabivitrina was introduced by Thiele (1931) as a section of the subgenus *Vitrina (Insulivitrina)*. Later, Hubendick (1953) regarded it as a junior synonym of *Vitrina (Phenacolimax)* and Forcart (1957, 1978) as a sugbenus of *Phenacolimax*. Recently, Schileyko (1986, 2003), Neubert (1998), Alonso et al. (2000) and Hausdorf (2002) accepted *Arabivitrina* as a distinct genus. Neubert (1998) reinvestigated the type species and concluded that *Arabivitrina* was close to *Insulivitrina*.

Hausdorf (2002) assigned seven species from SW Arabia, Abyssinia, Kenya and Uganda to *Arabivitrina* (major anatomical references on which are: Hesse, 1923; Thiele, 1933; Hubendick, 1953; Forcart, 1957; Neubert, 1998). He found that *Arabivitrina* was the sister group of *Calidivitrina* and that *Arabivitrina* plus *Calidivitrina* were, in turn, the sister group of *Plutonia* plus *Oligolimax*.

Only a few of the seven species assigned to *Arabivitrina* (Hausdorf, 2002) are known in detail anatomically. In most cases, available data only concerns the general scheme of the genitalia, so that major features of the internal structure of the penis and glandula amatoria are unknown or insufficiently described.

Besides the type species, we studied another species anatomically: *A. jansseni* from the Arabian peninsula. Apart from conchological differences (shell more globose, last whorl less dilated, aperture subcircular), it differs from the type species in minor anatomical details (free oviduct long and slender vs. very short and wide; vagina very long vs. vagina long; glandula amatoria one quarter of vagina length vs. half vagina length; penis long and slender vs. rather short). No substantial differences in internal structure of the penis were found in the two species

This group of vitrinids is relatively unknown: since many species have only been studied summarily, a thorough survey is needed. Moreover, there is no clear evidence that it is a monophyletic group, although BI analysis recovered the two species of this genus examined (*A. arabica* and *A. jansseni*) as a monophyletic group on the basis of one, non exclusive synapomorphy: the absence of a penial sheath (Table 3).

***Azorivitrina*, new genus**

Type Species: *Vitrina laxata* Morelet, 1860.

Material Examined

Azorivitrina brevispira (Morelet, 1860) – Portugal: Ilha de Santa Maria (Azores), Pico Alto, A. M. F. Martins leg. 9.10.1975 (3 spirit specimens, FGC).

Azorivitrina brumalis (Morelet, 1860) – Portugal: Ilha de São Miguel (Azores), Agua d'Alto, A. M.

F. Martins leg. 23.9.1970 (9 spirit specimens, FGC); Ilha de Pico (Azores), Cabeço da Urze, A. M. F. Martins leg. 13.2.1995 (5 spirit specimens, FGC).

Azorivitrina finitima (Morelet, 1860) – Portugal: Ilha de Flores (Azores), Ribeira dos Ilhéus, A. M. F. Martins leg. 16.10.1993 (1 spirit specimen, FGC).

Azorivitrina laxata (Morelet, 1860) – Portugal: Ilha de São Miguel (Azores), Falca, Santa Iria, A. M. F. Martins leg. 23.10.2006 (3 spirit specimens, FGC); Ilha de São Miguel (Azores), Porto Formoso, A. M. F. Martins leg. 23.11.2005 (3 spirit specimens, FGC); Ilha de São Miguel (Azores), Sete Cidades, Cumieira, A. M. F. Martins leg. 7.12.2005 (1 spirit specimen, FGC).

Diagnosis

Semislug-like vitrinids characterized by long penial retractor muscle arising from diaphragm, running in front of right optic nerve, below right ommatophore retractor and ending on penial complex subapically; stimulator consisting of glandula amatoria (absent in *A. brevispira*) with complete external glandular covering; penial complex with penial gland and without penial sheath (present in *A. finitima*); vas deferens entering penial complex medially or subapically (in *A. finitima*); internal structures of penial complex comprising main and accessory pilasters; main pilaster consisting of proximal glandular roll, distally lamellate or otherwise; accessory pilaster proximally funnel-like or pouch-like.

Description of Type Species

Shell: vitriniform slightly dilated, glossy, thin and fragile, depressed, with approximately 3.0 whorls, last whorl expanded; aperture wide with columellar and basal margins bordered by narrow periostracal fringe; columellar margin normal; umbilicus open, punctiform; protoconch slightly prominent, smooth, with many regular spiral rows of very small pits; teleoconch with faint radial growth lines (Mordan & Martins, 2001: figs. 2C, 7A–F).

Body: cannot be withdrawn completely into shell; right shell lobe large, covering wide portion of shell when animal undisturbed (Mordan & Martins, 2001: fig. 8A).

Radula: dichoglossan; marginal teeth bicuspid (Mordan & Martins, 2001: 355).

Female Distal Genitalia (Figs. 19, 20): free oviduct short and wide. Bursa copulatrix small and oval, with short to medium, more or less slender duct, initially not flared. Vagina with large oval glandula amatoria constituting about one third of its length. Glandula amatoria with very thick muscular wall, completely covered by external glandular layer; papilla of glandula amatoria short. Internal surface of distal vagina with longitudinal pleated pilaster starting from base of papilla of glandula amatoria and ending near genital atrium and low, sparse, mainly transverse pleats.

Male Distal Genitalia (Figs. 19, 20): penial complex small and club-like, with penial gland and without penial sheath. Penial gland partly covering side of proximal penial complex facing vagina. Penial retractor arising from diaphragm, long, inserted subapically. Vas deferens medium in length, entering penial complex about medially, thus distinguishing short stout flagellum and penis proper. Internal structures of penial complex comprising main pilaster and accessory pilaster. Main pilaster consisting of large proximal glandular roll, distally lamellate. Accessory pilaster short, arising funnel-like on one side of glandular roll and ending in proximal genital atrium. Vas deferens opening in transverse slit on glandular roll at about half its length. Internal surface smooth.

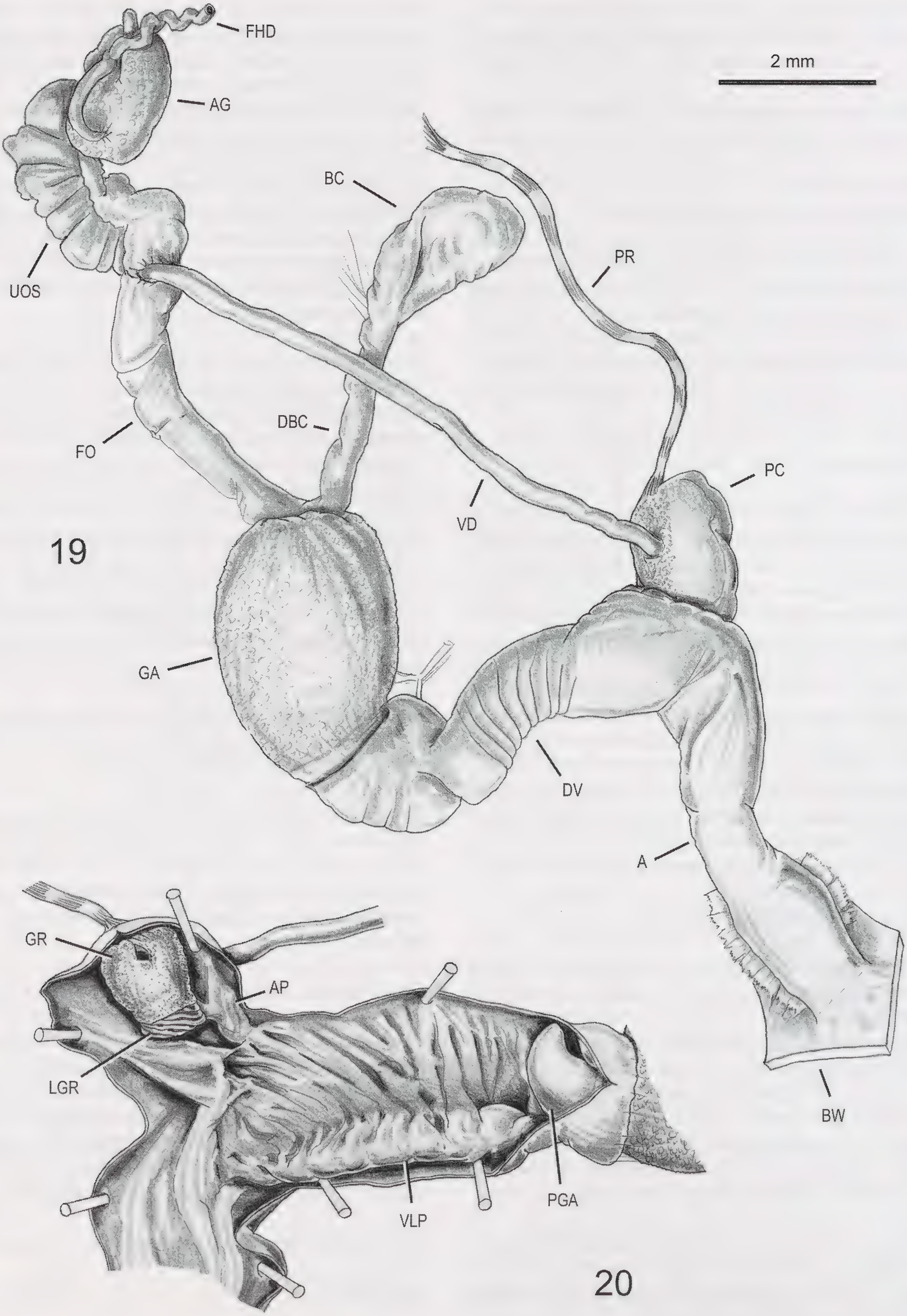
Genital Atrium (Figs. 19, 20): very long and cylindrical, with opposite sides connected to body wall by robust muscular bands. Internal structures consisting of distal portion of main and accessory pilasters. Internal surface smooth.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: similar in juveniles and adults (Fig. 3). Penial retractor long, passing between fork formed by retractors of right ommatophore and right lower tentacle, around right ocular nerve, then backwards to end on diaphragm; distal genitalia lying right of right ommatophore retractor which therefore appears free of penial complex and vagina.

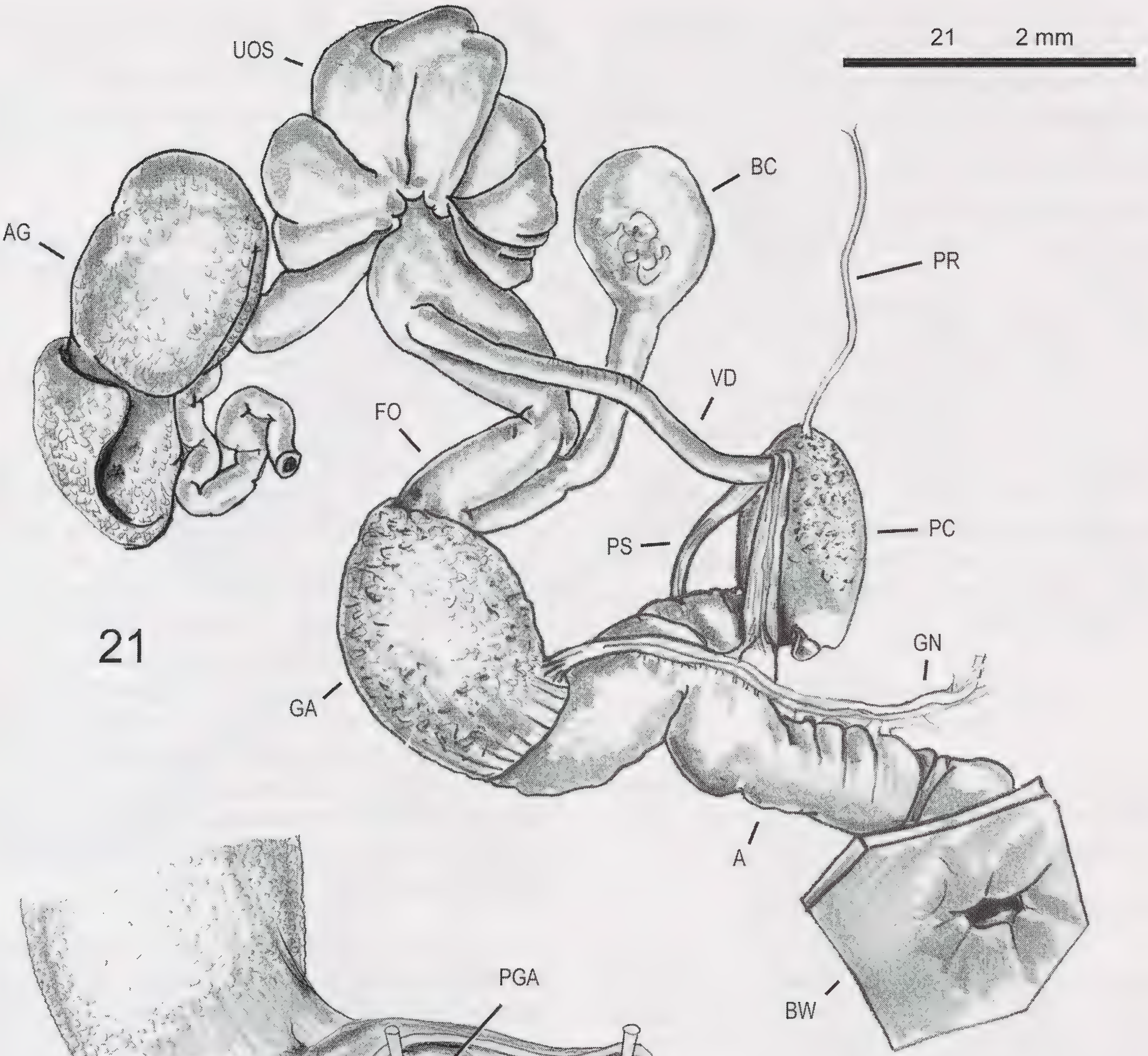
Mating: no data available.

Remarks

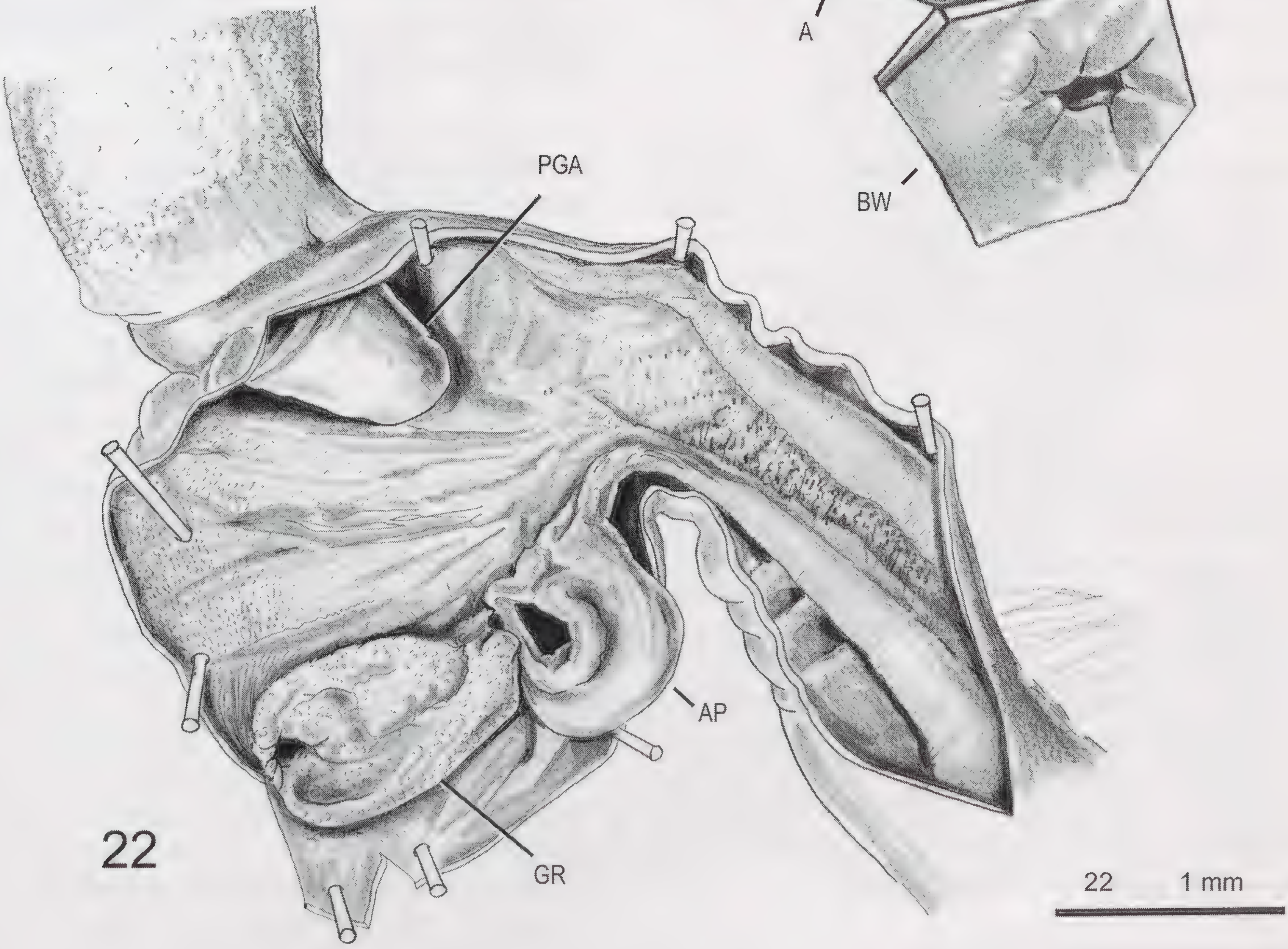
All four species of Azorean vitrinids re-examined by us share an accessory pilaster arising on one side (*A. laxata*) or at distal end



FIGS. 19, 20. *Azorivitrina laxata* (Morelet, 1860) from Ilha de São Miguel, Sete Cidades, Cumieira (Azores, Portugal), A. M. F. Martins leg. 7.12.2005. FIG. 19: Distal genitalia; FIG. 20: Internal structure of distal genitalia.



21



22

FIGS. 21, 22. *Azorivitrina finitima* (Morelet, 1860) from Ilha de Flores, Ribeira dos Ilhéus (Azores, Portugal), A. M. F. Martins leg. 16.10.1993. FIG. 21: Distal genitalia; FIG. 22: Internal structure of distal genitalia.

(*A. brevispira*, *A. brumalis* and *A. finitima*) of glandular roll with funnel-like or pouch-like structure. Phylogenetic analysis confirmed that the species of *Azorivitrina* constitute a variably supported monophyletic group (Figs. 14, 15; Table 3). We interpreted the unique structure of the accessory pilaster as a synapomorphy supporting an Azorean monophyletic group of vitrinids.

Apart from *A. brumalis*, the other *Azorivitrina* species differ noticeably from the type species. *A. finitima* is characterized by a penial complex having a slender penial sheath, a thin penial retractor (sometimes absent) and main pilaster consisting of a glandular roll, not lamellate distally (Figs. 21, 22). *A. brevispira* lacks glandula amatoria and has a large penial complex with a well developed glandular roll having a distal portion with small thorny papillae (Figs. 23, 24).

Canarivitrina Valido & Alonso
in: Alonso et al., 2000

Type Species: *Plutonia (Canarivitrina) taburientensis* Groh & Valido in: Alonso et al., 2000, by original designation.

Material Examined

Canarivitrina taburientensis (Groh & Valido in Alonso et al., 2000) – Spain: La Palma Island (Canary Islands), Caldera de Taburiente, 28RBS1879, M. R. Alonso & M. Ibáñez leg. 8.1.1988 (1 spirit specimen, FGC).

Diagnosis

Semislug-like vitrinids characterized by long penial retractor muscle arising from diaphragm, running in front of right optic nerve, below right ommatophore retractor and ending on penial complex subapically; stimulator consisting of glandula amatoria with complete external glandular covering; penial complex with penial gland and without penial sheath; vas deferens entering penial complex medially or distally; internal structures of penial complex distinctive and consequently difficult to homologize, comprising glandular roll, papilla-like structure, muscular pleat and laminar crest.

Description of Type Species

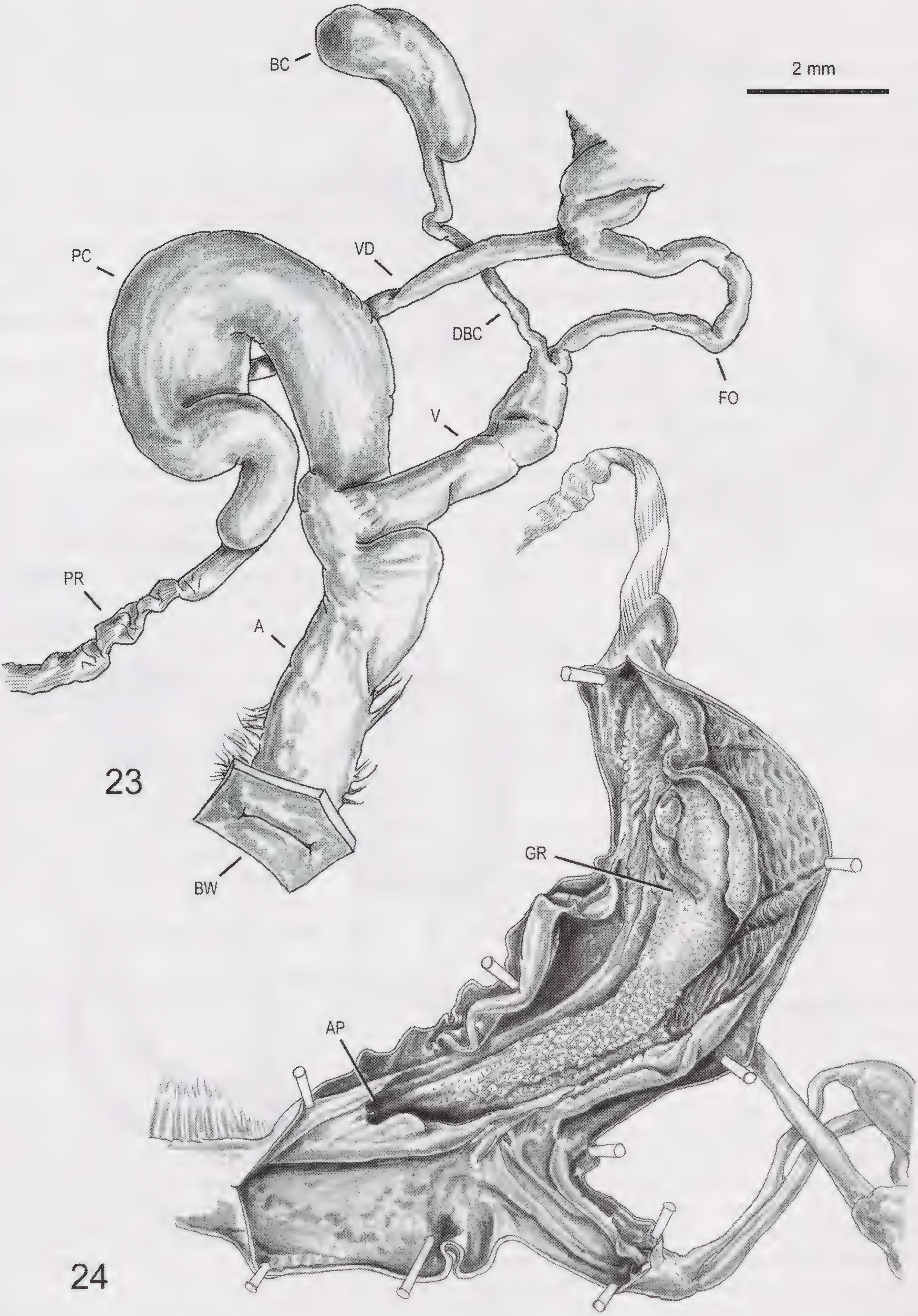
Shell: vitriniform slightly dilated, glossy, thin and fragile, depressed, with approximately 2.5 whorls; last whorl well expanded; aperture wide with columellar and basal margins bordered by broad periostracal fringe; columellar margin normal; umbilicus closed; protoconch not prominent, smooth, with many regular spiral rows of very small pits; teleoconch smooth (Alonso et al., 2000: figs. 2A, E).

Body: cannot be withdrawn completely into shell; right shell lobe large, covering wide portion of shell when animal undisturbed.

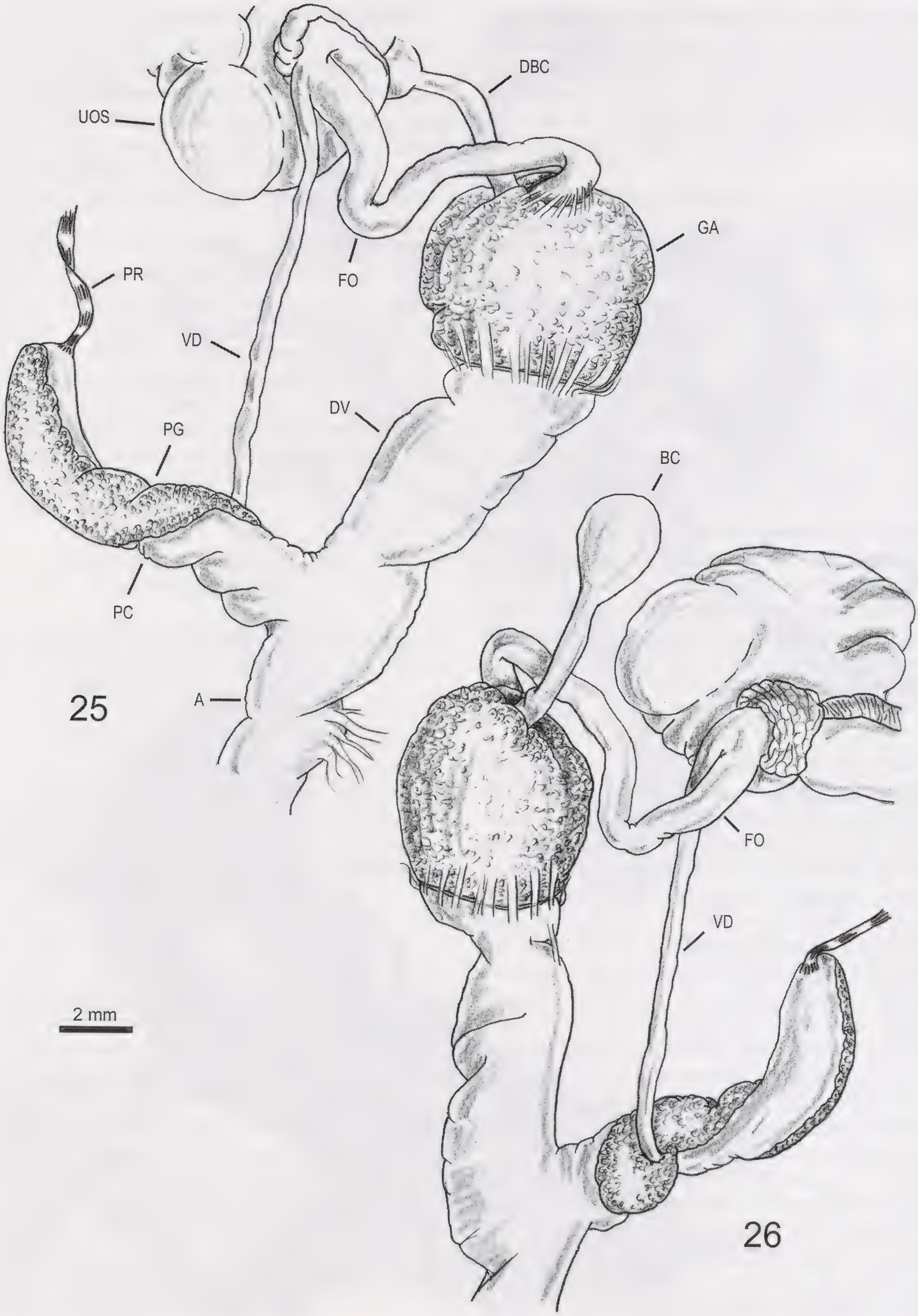
Radula: dichoglossan; marginal teeth unicuspid (Alonso et al., 2000: 50).

Female Distal Genitalia (Figs. 25–28): free oviduct long and slender. Bursa copulatrix small and oval, with short, more or less slender duct, initially not flared. Vagina long, with small bulbous glandula amatoria constituting about one third of its length. Glandula amatoria with very thick muscular walls, completely covered by external glandular layer; papilla of glandula amatoria very short. Internal surface of distal vagina with low irregular transverse pleats and two longitudinal pleated pilasters starting from base of papilla of glandula amatoria and ending near genital atrium (the shorter one) or in genital atrium (the longer one).

Male Distal Genitalia (Figs. 25–28): penial complex large and finger-like (sometimes twisted on itself), with penial gland and without penial sheath. Penial gland covering one side of penial complex. Penial retractor arising from diaphragm, very long, inserted subapically. Vas deferens medium in length, entering penial complex subdistally, thus distinguishing long pointed flagellum and short penis proper. Internal structures of penial complex distinctive, and consequently difficult to homologize, comprising glandular roll, papilla-like structure, muscular pleat and laminar crest (glandular roll - muscular pleat and laminar crest presumably homologous with main and accessory pilasters, respectively). Long slender, not distally lamellate, glandular roll ("torus"; Alonso et al., 2000) located in correspondence with penial gland and ending at base of small cylindrical papilla-like structure. Short, superficially pleated muscular pleat arising distally in respect to papilla-like structure and ending in proximal genital atrium. Long, thin, rolled, laminar crest ("velum"; Alonso et al., 2000) running parallel on opposite side to glandular roll. Vas deferens opening at tip of papilla-like structure. Internal surface with thin, mainly transverse pleats and diffuse spongy glandular tissue with crypts or smooth.



FIGS. 23, 24. *Azorivitrina brevispira* (Morelet, 1860) from Ilha de Santa Maria, Pico Alto (Azores, Portugal), A. M. F. Martins leg. 9.10.1975. FIG. 23: Distal genitalia; FIG. 24: Internal structure of distal genitalia.



FIGS. 25, 26. Distal genitalia of a specimen of *Canarivitrina taburientensis* (Groh & Valido in: Alonso et al., 2000) from La Palma Island, Caldera de Taburiente (Canary Islands, Spain), M. R. Alonso & M. Ibáñez leg. 8.1.1988.

Genital Atrium (Figs. 25–28): short, with one side connected to body wall by thin muscular bands. Internal structure consisting of short pilaster and distal portion of larger vaginal pilaster. Internal surface as in distal vagina.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: similar in juveniles and adults (Fig. 3). Penial retractor very long, passing below right ommatophore and in front of right optic nerve; distal genitalia lying right of right ommatophore retractor which therefore appears free of penial complex and vagina.

Mating: no data available.

Remarks

Alonso et al. (2000) recently described *Canarivitrina* for five species from the Canary Islands that shared some penial characters. They also discovered that *Canarivitrina* shares relationships between penial retractor and right ommatophore retractor with the other Macaronesian vitrinids (*Guerrina*, *Insulivitrina*, *Madeirovitrina* and *Plutonia*) and therefore lumped them into a single genus (*Plutonia*), ranking *Canarivitrina* and the other genus-group taxa as subgenera.

Canarivitrina constitutes one of the best defined monophyletic groups among Macaronesian vitrinids, supported by at least one-two exclusive synapomorphies of the penial complex (Figs. 14, 15; Table 3), though its deep relationships remain unresolved.

Guerrina Odhner, 1954

Type Species: *Helix cuticula* Shuttleworth, 1852, by monotypy.

Material Examined

Guerrina cuticula (Shuttleworth, 1852) – Spain: Tenerife Island (Canary Islands), Barranco del Agua, M. R. Alonso & M. Ibáñez leg. 12.12.1984 (2 spirit specimens, FGC); Tenerife Island (Canary Islands), El Roquillo, M. R. Alonso & M. Ibáñez leg. 24.4.1984 (2 spirit specimens, FGC).

Diagnosis

Snail-like vitrinids characterized by long penial retractor muscle arising from diaphragm, running in front of right optic nerve, below right ommatophore retractor and ending on penial complex subapically or laterally; stimulator consisting of glandula amatoria with incomplete external glandular covering; penial complex with penial gland and without penial sheath; vas deferens entering penial complex medially; internal structures of penial complex comprising only main pilaster, consisting of large, distally lamellate, proximal glandular roll and distal muscular pleat.

Description of Type Species

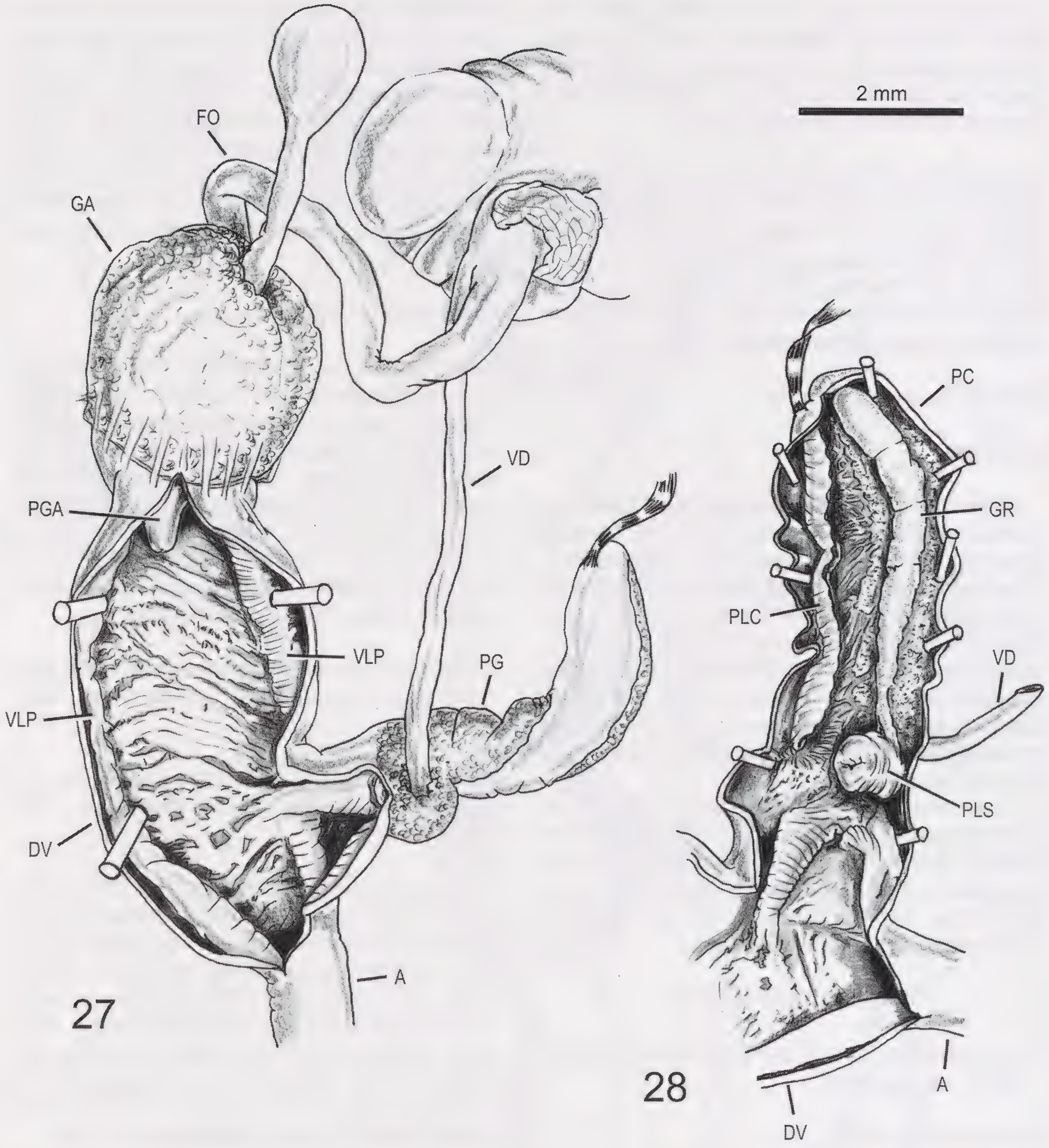
Shell: trochiform, translucent, thin and fragile, conical-depressed, sharply keeled, with approximately 3.0 whorls; last whorl expanded; aperture moderately wide with margin not bordered by periostracal fringe; columellar margin normal; umbilicus closed; protoconch prominent, with fine, closely spaced, radial riblets and large pits inbetween; teleoconch with fine, closely and regularly spaced, slightly wavy, radial riblets (Ibáñez et al., 1987: figs. 32, 38, 39).

Body: can be withdrawn completely into shell; right shell lobe absent (Ibáñez et al., 1987: fig. 3).

Radula: dichoglossan; marginal teeth unicuspid (Odhner, 1954: 57, fig. 2; Ibáñez et al., 1987: 124, fig. 19).

Female Distal Genitalia (Figs. 29–31): free oviduct short to long and slender. Bursa copulatrix small and oval to globular, with short to long, very slender duct, initially not flared. Vagina long, with small heart-like glandula amatoria constituting about one third of its length. Glandula amatoria with very thick muscular wall, covered only proximally; papilla of glandula amatoria very short. Internal surface of distal vagina with low mainly transverse pleats.

Male Distal Genitalia (Figs. 29–31): penial complex small and club-like, with penial gland and without penial sheath. Penial gland covering most of penial complex. Penial retractor arising from diaphragm, long, inserted apically. Vas deferens medium in length, entering penial complex medially inside deep constriction, thus distinguishing short, pointed flagellum and penis proper. Internal structures of penial complex comprising main pilaster only which consists of large proximal glandular roll, distally lamellate, and smooth distal muscular pleat, ending in proximal genital atrium. Vas deferens opening

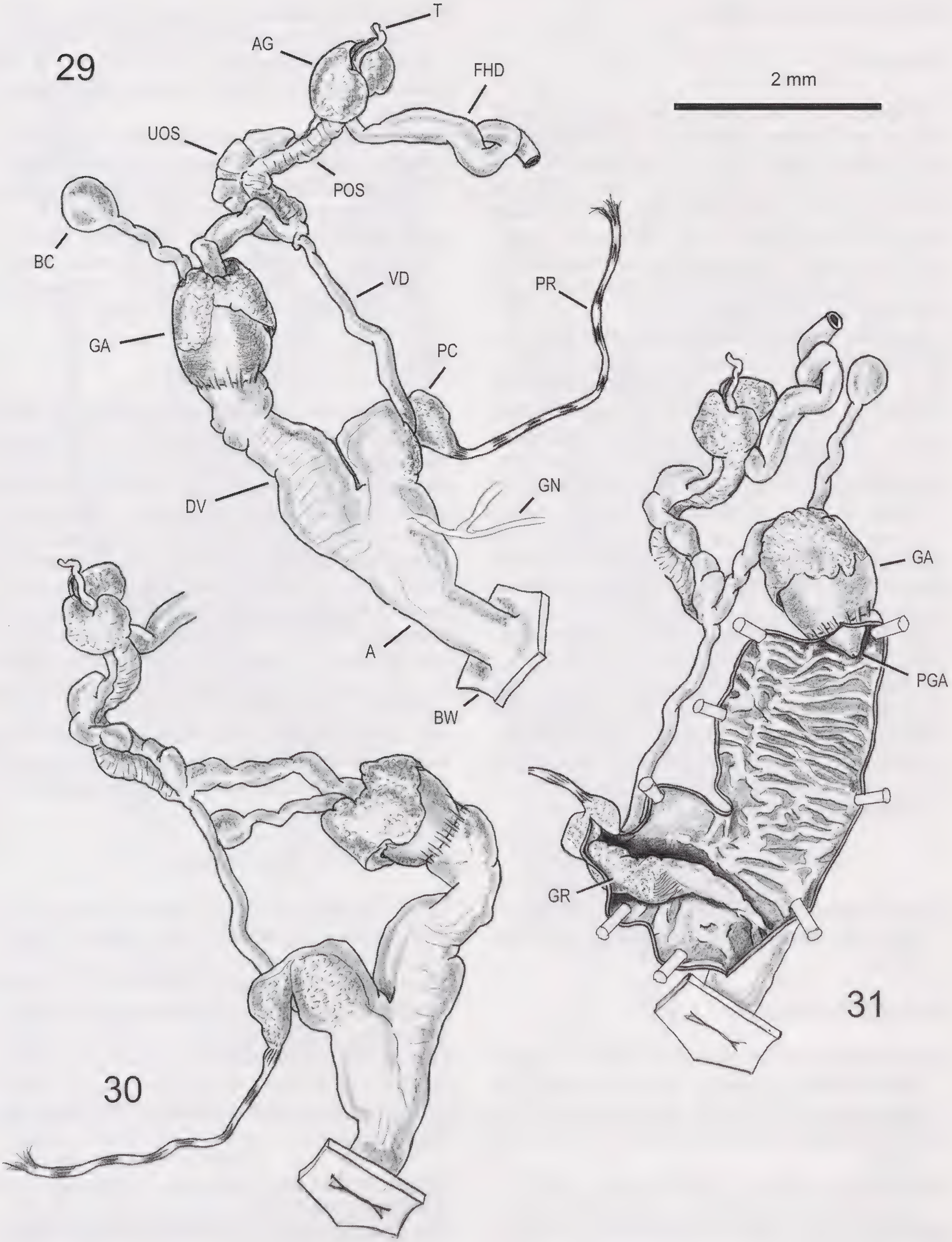


FIGS. 27, 28. *Canarivitrina taburientensis* (Groh & Valido in: Alonso et al., 2000) from La Palma Island, Caldera de Taburiente (Canary Islands, Spain), M. R. Alonso & M. Ibáñez leg. 8.1.1988. FIG. 27: Internal structure of vagina; FIG. 28: Penial complex.

not visible, probably level with glandular roll. Internal surface smooth.

Genital Atrium (Figs. 29–31): long and funnel-like, with one side connected to body wall by thin muscular bands. Internal structure consisting of distal portion of main pilaster. Internal surface as in penial complex.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: similar in juveniles and adults (Fig. 3). Penial retractor long, passing below right ommatophore and in front of right optic nerve; distal genitalia lying right of right ommatophore retractor which therefore appears free of penial complex and vagina.



FIGS. 29–31. *Guerrina cuticula* (Shuttleworth, 1852) from Tenerife Island, Barranco del Agua (Canary Islands, Spain), M. R. Alonso & M. Ibáñez leg. 12.12.1984. FIGS. 29, 30: Distal genitalia; FIG. 31: Internal structure of penial complex and vagina.

Mating: no data available.

Remarks

Guerrina was established as a subgenus of *Vitrina* by Odhner (1954) for a species from the Canary Islands. Later it was regarded as a subgenus of *Phenacolimax* by Zilch (1959), a distinct genus by Schileyko (1986, 2003), Ibáñez et al. (1987) and Valido et al. (1993) and, finally, a subgenus of *Plutonia* by Alonso et al. (2000) and Hausdorf (2002) (for other comments, see Remarks on *Canarivitrina*).

Guerrina includes only two species from the Canary Islands: *G. christinae* (Groh in: Valido et al., 1993) and *G. cuticula* (major anatomical references on which are: Odhner, 1954; Ibáñez et al., 1987; Valido et al., 1993), which differ in a number of anatomical characters (penial complex with short pointed flagellum; penial retractor inserted at apex of flagellum; marginal teeth unicuspid in *G. cuticula*; penial complex with large globular flagellum; penial retractor inserted laterally half way along penial complex; marginal teeth pluricuspid in *G. christinae*; for *G. cuticula*: Figs. 29–31; Ibáñez et al., 1987; Valido et al., 1993; for *G. christinae*: Valido et al., 1993).

Alonso et al. (2000) regarded *Guerrina* as a monophyletic group based on the fact that it can withdraw into its shell. Indeed all analyses recovered *Guerrina* as monophyletic, supported by at least one non exclusive synapomorphy: snail habitus (Figs. 14, 15; Table 3).

Insulivitrina Hesse, 1923

Type Species: *Helicolimax lamarckii* Férussac, 1821, by subsequent designation (Hesse, 1924).

Material Examined

Insulivitrina lamarckii (Férussac, 1821) – Spain: Tenerife Island (Canary Islands), Vueltas de Taganana, 28RCS8158, M. R. Alonso & M. Ibáñez leg. 19.12.1988 (4 spirit specimens, FGC).

Insulivitrina blauneri (Shuttleworth, 1852) – Spain: Tenerife Island (Canary Islands), Barranco del Agua, M. R. Alonso & M. Ibáñez leg. 12.12.1984 (2 spirit specimens, FGC).

Insulivitrina canariensis (Mousson, 1872) – Spain: El Hierro Island (Canary Islands), Fuente de Mencáfete, M. J. Valido leg. 15.5.1984 (2 spirit specimens, FGC).

Insulivitrina eceroensis Alonso & Ibáñez, 1987 – Spain: El Hierro Island (Canary Islands), Fuente de Mencáfete, M. R. Alonso & M. Ibáñez leg. 15.5.1984 (3 spirit specimens, FGC).

Insulivitrina gomerensis Alonso & Ibáñez, 1988 – Spain: La Gomera (Canary Islands), Montaña Quemada, K. Groh & M. Ibáñez leg. 2.1.1988 (4 spirit specimens, FGC).

Insulivitrina oromii Ibáñez & Alonso, 1988 – Spain: La Gomera (Canary Islands), Montaña de la Zarza, K. Groh & M. Ibáñez leg. 3.1.1988 (1 spirit specimen, FGC).

Diagnosis

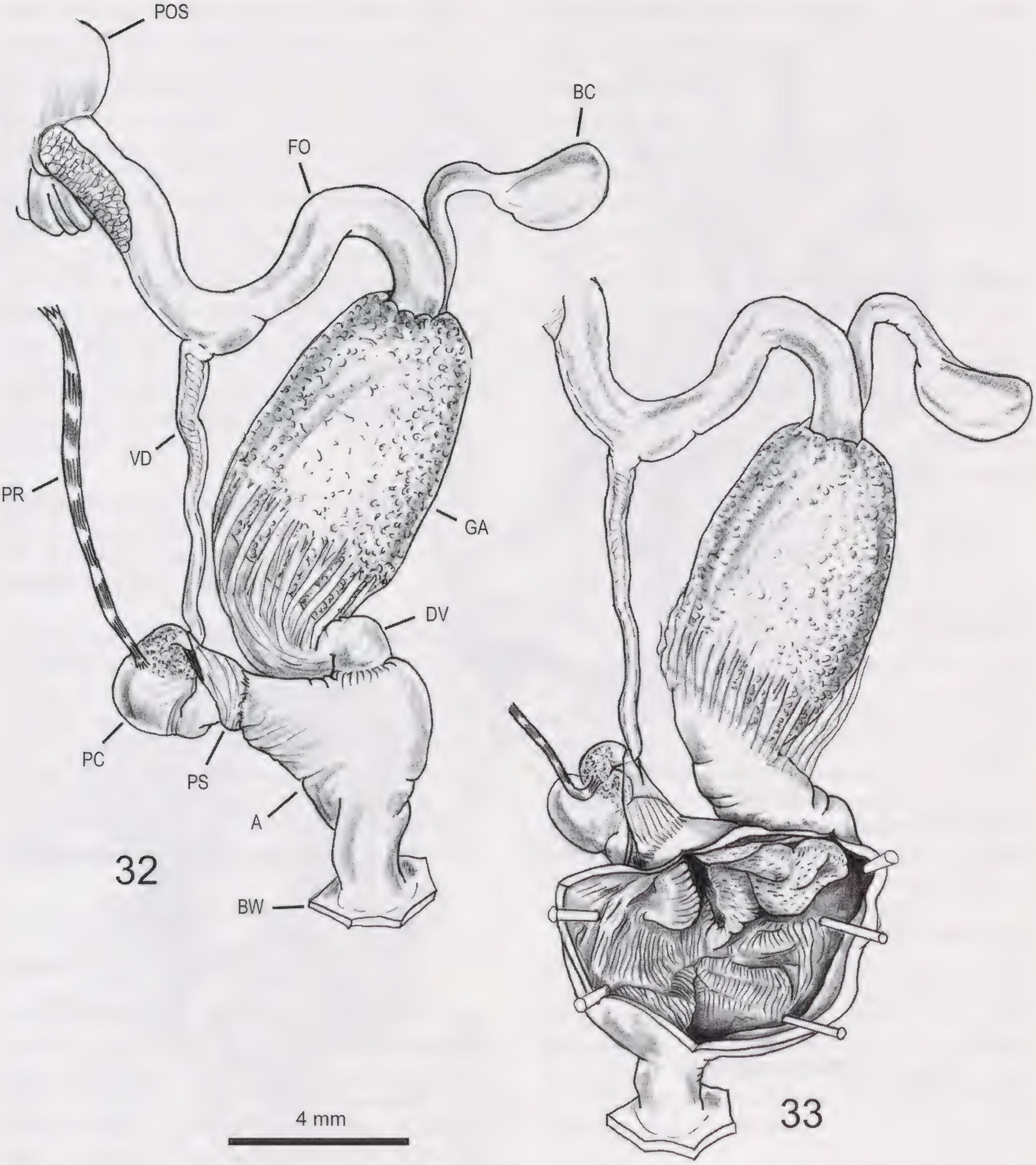
Semislug-like vitrinids characterized by long penial retractor muscle arising from diaphragm, running in front of right optic nerve, below right ommatophore retractor and ending on penial complex subapically; stimulator consisting of glandula amatoria with complete external glandular covering; penial complex with penial gland and reduced penial sheath (absent in many species); vas deferens contacting penial complex medially, traversing penial sheath and entering it apically or subapically (when penial sheath absent, vas deferens entering penial complex apically or subapically); internal structures of penial complex comprising two distinctive pilasters, possibly homologous with main and accessory pilasters (at least in type species).

Description of Type Species

Shell: vitriniform very dilated, glossy, thin and fragile, depressed, with approximately 2.5 whorls; last whorl extremely expanded; aperture very wide with columellar and basal margins bordered by broad periostracal fringe; columellar margin normal; umbilicus closed; protoconch not prominent, smooth, with many regular spiral rows of very small pits; teleoconch smooth (Ibáñez et al., 1987: figs. 33, 40, 41).

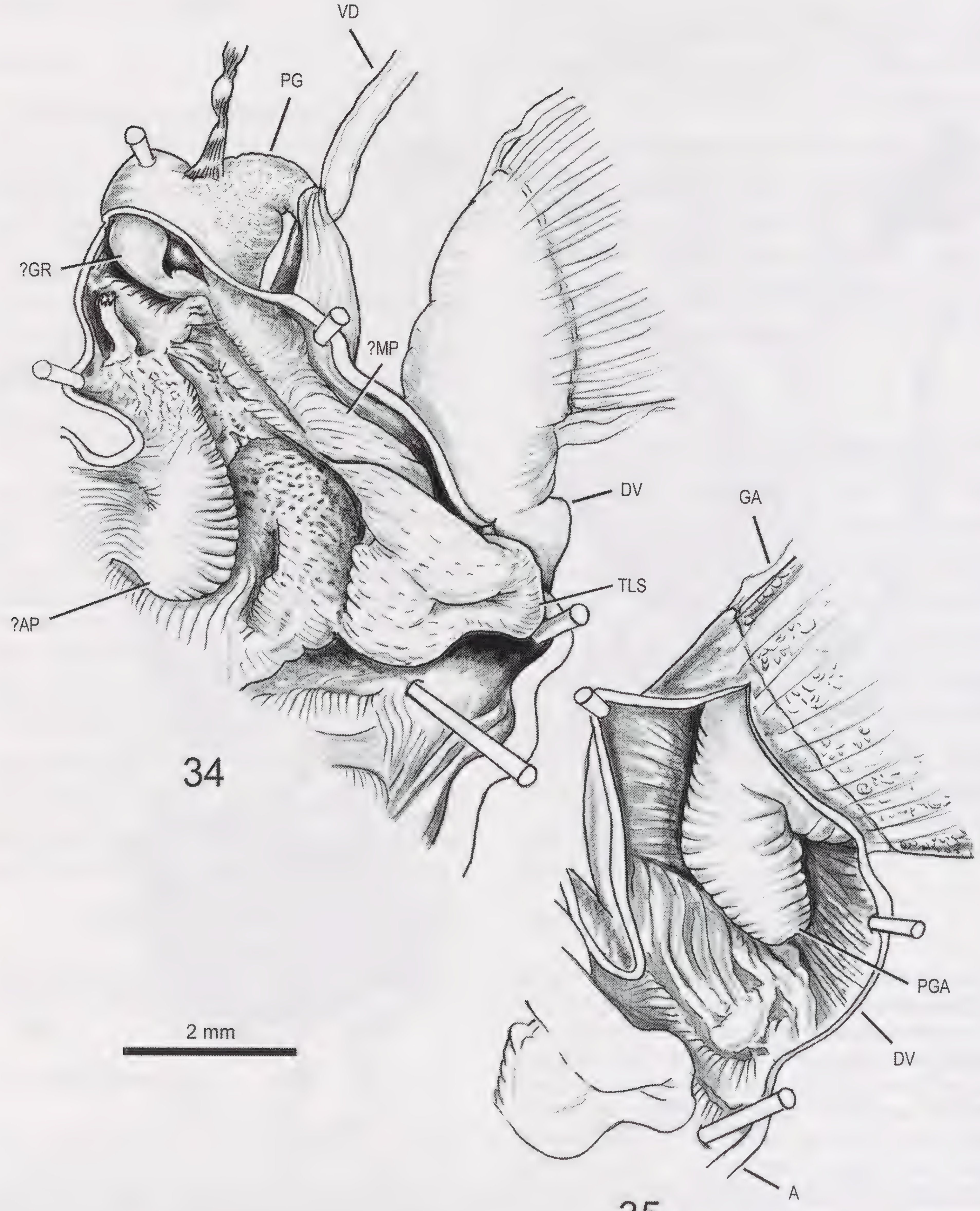
Body: cannot be withdrawn completely into shell; right shell lobe large, covering wide portion of shell when animal undisturbed (Ibáñez et al., 1987: fig. 4).

Radula: dichoglossan; marginal teeth bicuspid (with one small ectocone) (Hesse, 1923: 135, pl. 2, fig. 18; Ibáñez et al., 1987: 129, fig. 22).



FIGS. 32, 33. *Insulivitrina lamarckii* (Férussac, 1821) from Tenerife Island, Vueltas de Taganana (Canary Islands, Spain), M. R. Alonso & M. Ibáñez leg. 19.12.1988. FIG. 32: Distal genitalia; FIG. 33: Internal structure of penial complex.

Female Distal Genitalia (Figs. 32–35): free oviduct short to long and wide. Bursa copulatrix small and oval, with short to medium, more or less slender duct, initially not flared. Vagina long, with large oval glandula amatoria constituting about 2/3 of its length. Glandula amatoria with very thick muscular wall, completely covered by external glandular layer; papilla of glandula amatoria long. Internal surface of distal vagina with irregular low transverse pleats and sort of pad bordering opening into genital atrium.



FIGS. 34, 35. *Insulivitrina lamarckii* (Férussac, 1821) from Tenerife Island, Vueltas de Taganana (Canary Islands, Spain), M. R. Alonso & M. Ibáñez leg. 19.12.1988. FIG. 34: Internal structure of penial complex; FIG. 35: Vagina.

Male Distal Genitalia (Figs. 32–35): penial complex small and globular, with penial gland and penial sheath. Penial gland covering side of proximal penial complex facing vagina. Penial sheath short, arising from mid penial complex. Penial retractor arising from diaphragm, long, inserted subapically. Vas deferens medium in length, contacting penial complex medially, then traversing penial sheath and entering penial complex apically near insertion of penial retractor. Internal structures of penial complex comprising two distinctive pilasters, possibly homologous with main and accessory pilasters. Larger pilaster (main pilaster?) consisting of proximal glandular crest (modified glandular roll?), rolled upon itself and distally transversely pleated and distal muscular pleat ending in sort of tongue-like structure bent to one side as if closing distal vagina. Smaller pleated crest (accessory pilaster?) arising near rolled crest and ending before genital atrium. Vas deferens opening encircled by rolled glandular crest. Internal surface with low, irregularly arranged pleats and sparse spongy tissue with crypts.

Genital Atrium (Figs. 32–35): long and funnel-like, with one side connected to body wall by thin muscular bands. Internal surface as in penial complex.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: similar in juveniles and adults (Fig. 3). Penial retractor long, passing between fork formed by retractors of right ommatophore and right lower tentacle, around right ocular nerve, then backwards to end on diaphragm; distal genitalia lying right of right ommatophore retractor which therefore appears free of penial complex and vagina.

Mating: no data available.

Remarks

Insulivitrina was introduced by Hesse (1923) for four species from the Macaronesian islands (Madeira, Azores and Canary Islands) and one from the Arabian Pensinsula. The status and relationships of *Insulivitrina* have intrigued many authors: it was regarded as a distinct genus by Hoffmann (1929), Forcart (1944) and Odhner (1954), a subgenus of *Vitrina* by Thiele (1931), a junior synonym of *Phenacolimax* by Hubendick (1953), a subgenus of *Phenacolimax* by Forcart (1957), Zilch (1959) and Backhuys (1975), again a distinct genus by Schileyko (1986, 2003), Ibáñez et al. (1987) and Valido et al. (1990, 1993), a junior synonym of *Oligolimax* by Manganelli et al. (1995) and, finally, a subgenus of *Plutonia* by Alonso et al. (2000) and Hausdorf (2002).

According to Hausdorf (2002), *Insulivitrina* includes 20 species (major anatomical references on which are: Schileyko, 1986; Alonso et al., 1987; Ibáñez et al., 1987; Morales et al., 1988; Valido et al., 1990; Mordan & Martins, 2001) all from the Azores and Canary Islands and "is a paraphyletic group from which the other, more specialized Macaronesian groups are derived" (Hausdorf, 2002: 348). However the Azorean species belong to a monophyletic group exclusive to this archipelago, at least those examined by us.

Schileyko (1986: fig. 2) studied the anatomy of a specimen from Tenerife assigned to *I. teneriffae* (Quoy & Gaimard, 1832), a junior synonym of *I. lamarckii* (see: Bank et al., 2002). Actually, this specimen belongs to another species, perhaps *I. parryi* (Gude, 1896), from Gran Canaria, or *I. canariensis*, from El Hierro, according to M. R. Alonso and M. Ibáñez (pers. comm. 26.04.1999).

Besides the type species, five other species were examined: *I. blauneri* (Figs. 36–38), *I. canariensis*, *I. eceroensis*, *I. gomerensis* and *I. oromii.* They differ from the type species only by virtue of a few minor details. Hausdorf (2002) excludes presence of a penial sheath in the species of *Plutonia* (understood as including all Macaronesian vitrinids). Actually, the penial sheath is present, albeit reduced, in the type species of *Insulivitrina* (*I. lamarckii*) and in *I. blauneri*; other *Insulivitrina* species, such as *I. canariensis* and *I. oromii*, have bundles of fibres fastening wall of distal penial complex to those of terminal part of vas deferens which might be extreme residues of a penial sheath.

There is no evidence that *Insulivitrina* species constitute a monophyletic group (Figs. 14, 15; Table 3). However, as the *Insulivitrina* species are restricted to the Canary Islands, they could be a distinct Canarian monophyletic radiation of vitrinids, separate from *Canarivitrina* and *Guerrina*, or a paraphyletic group from which the other two are derived.

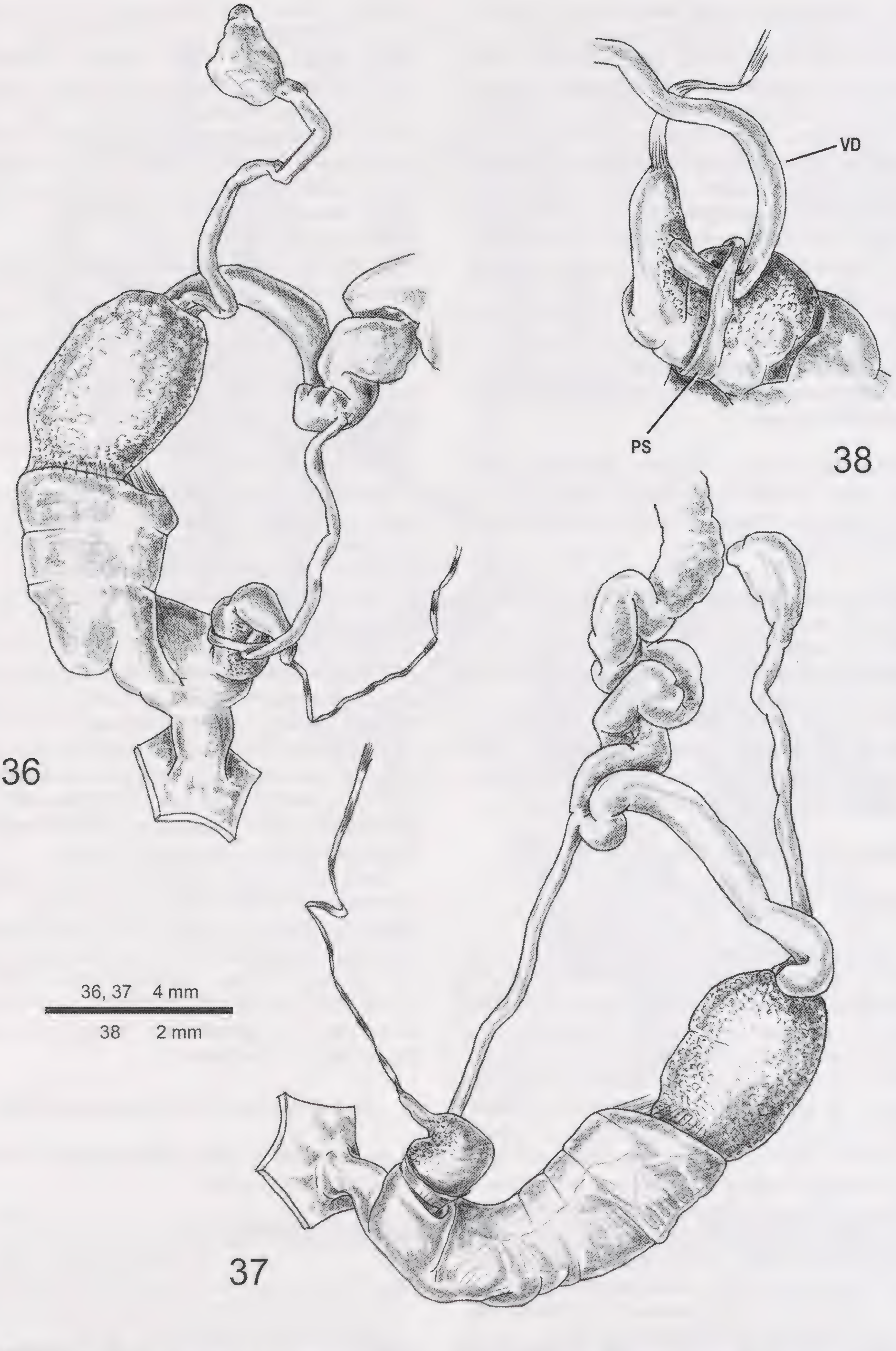
Madeirovitrina Groh & Hemmen, 1986

Type Species: *Vitrina nitida* Gould, 1847, by original designation.

Material Examined

Madeirovitrina nitida (Gould, 1847) – Portugal: Ilha da Madeira, Pico Ruivo, K. Groh leg. 7.1985 (2 spirit specimens, FGC).

Madeirovitrina marcida (Gould, 1847) – Portugal: Ilha da Madeira, Balcões, K. Groh leg. 6.1989 (2 spirit specimens, FGC).



FIGS. 36–38. *Insulivitrina blauneri* (Shuttleworth, 1852) from Tenerife Island, Barranco del Agua (Canary Islands, Spain), M. R. Alonso & M. Ibáñez leg. 12.12.1984. FIGS. 36, 37: Distal genitalia; FIG. 38: Detail of penial complex.

Diagnosis

Semislug-like vitrinids characterized by long penial retractor muscle arising from diaphragm, running in front of right optic nerve, below right ommatophore retractor and ending on penial complex subapically; stimulator consisting of glandula amatoria with complete external glandular covering; penial complex with penial gland and without penial sheath; vas deferens entering penial complex medially; internal structures of penial complex comprising main and accessory pilasters; main pilaster consisting of large, distally lamellate, proximal glandular roll and smooth, robust distal muscular pleat; accessory pilaster slender, bridge-like (its medial portion detached from genital walls as free cordon).

Description of Type Species

Shell: vitriniform slightly dilated, glossy, thin and fragile, depressed, with approximately 3.0 whorls; last whorl well expanded; aperture wide with columellar and basal margins bordered by broad periostracal fringe; columellar margin normal; umbilicus closed; protoconch not prominent, smooth, with many regular spiral rows of very small pits; teleoconch smooth (Groh & Hemmen, 1986: pl. 1, figs. 1, 2).

Body: available data controversial. According to Alonso et al. (2000), *Madeirovitrina* species cannot withdraw body completely into shell and right shell lobe is well developed, covering shell almost completely when animal undisturbed. However spirit specimens of *M. nitida* and *M. marcida* have body almost completely withdrawn into shell and small right shell lobe.

Radula: dichoglossan; marginal teeth bicuspid (Groh & Hemmen, 1986: 187, pl. 5, fig. 15b).

Female Distal Genitalia (Figs. 39, 40): free oviduct short and wide. Bursa copulatrix small and oval, with short, more or less slender duct, initially not flared. Vagina long, with large cylindrical glandula amatoria constituting about 2/3 of its length. Glandula amatoria with very thick muscular wall, completely covered by external glandular layer; papilla of glandula amatoria long. Internal surface of distal vagina with low, sparse, mainly transverse pleats.

Male Distal Genitalia (Figs. 39, 40): penial complex small and club-like, with penial gland and without penial sheath. Penial gland covering most of proximal penial complex. Penial retractor arising from diaphragm, long, inserted subapically. Vas deferens medium in length, entering penial complex about medially inside groove, thus distinguishing short stout flagellum and penis proper. Internal structures of penial complex comprising main pilaster and accessory pilaster. Main pilaster consisting of large proximal glandular roll, distally lamellate and smooth robust distal muscular pleat, ending in genital atrium, branching or otherwise, near gonopore. Accessory pilaster slender, bridge-like, arising on one side of glandular roll and ending near gonopore; remarkably, medial portion detached from genital walls as free cordon. Vas deferens opening in transverse slit on glandular roll at about half its length. Internal surface smooth.

Genital Atrium (Figs. 39, 40): long and cylindrical, with one side connected to body wall by robust muscular bands. Internal structures consisting of distal portion of main and accessory pilasters. Internal surface smooth.

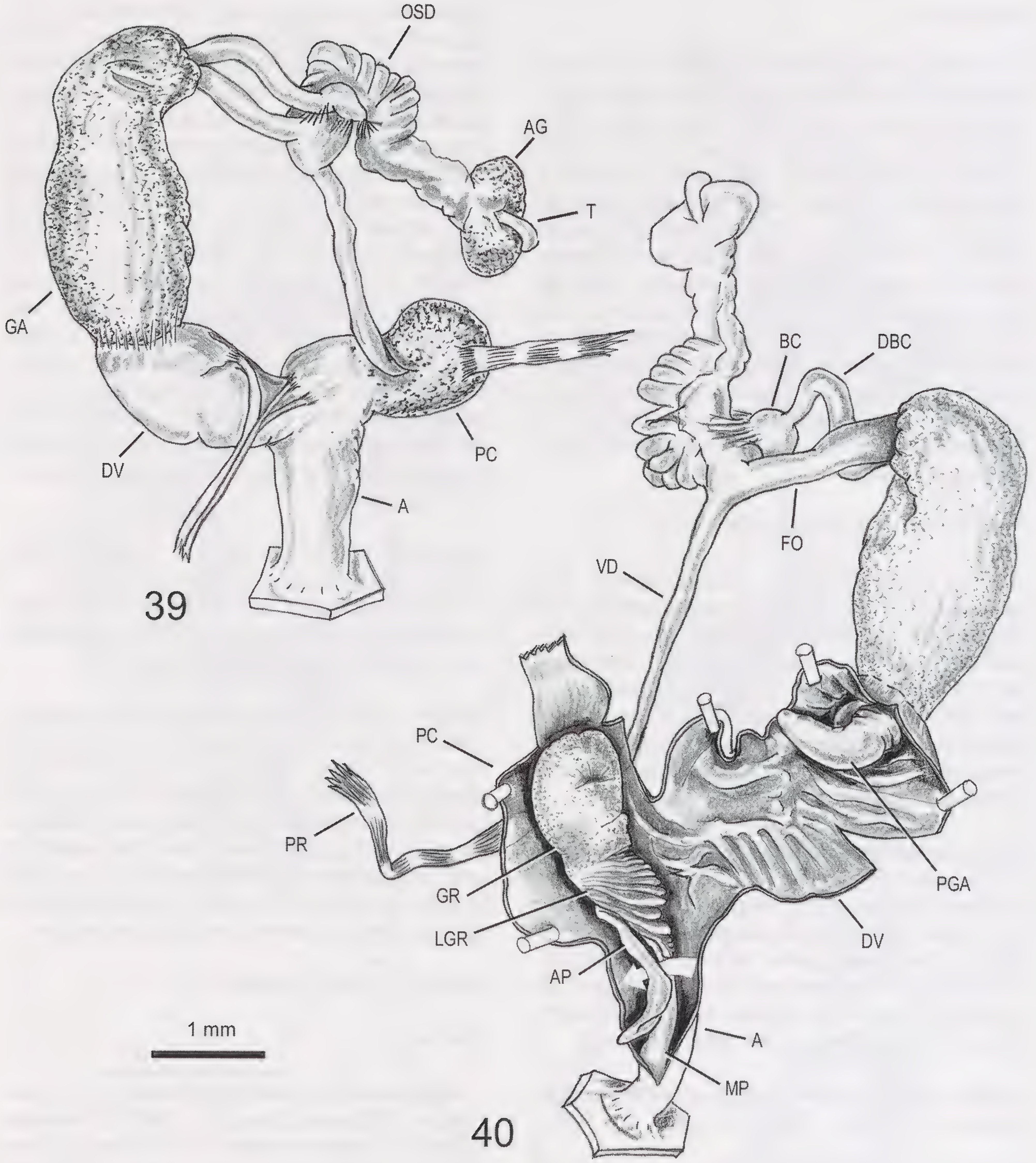
Relationships Between Right Ommatophore Retractor and Distal Genitalia: similar in juveniles and adults (Fig. 3). Penial retractor long, passing between fork formed by retractors of right ommatophore and right lower tentacle, around right ocular nerve, then backwards to end on diaphragm; distal genitalia lying right of right ommatophore retractor which therefore appears free of penial complex and vagina.

Mating: no data available.

Remarks

Madeirovitrina was established as a subgenus of *Phenacolimax* by Groh & Hemmen (1986) for some species from Madeira. It was recently regarded as a subgenus of *Plutonia* by Alonso et al. (2000) and Hausdorf (2002). Hausdorf (2002) assigned six species to *Madeirovitrina*, two only tentatively (one was assigned to *Eucobresia* by Groh & Hemmen, 1986) (major anatomical references on *Madeirovitrina* species: Odhner, 1937; Groh & Hemmen, 1986).

The vaginal retractor muscle (Vaginaretraktormuskel) described by Groh & Hemmen (1986) probably corresponds to the genital nerve which originates from the right pedal ganglion and ends with numerous branches on

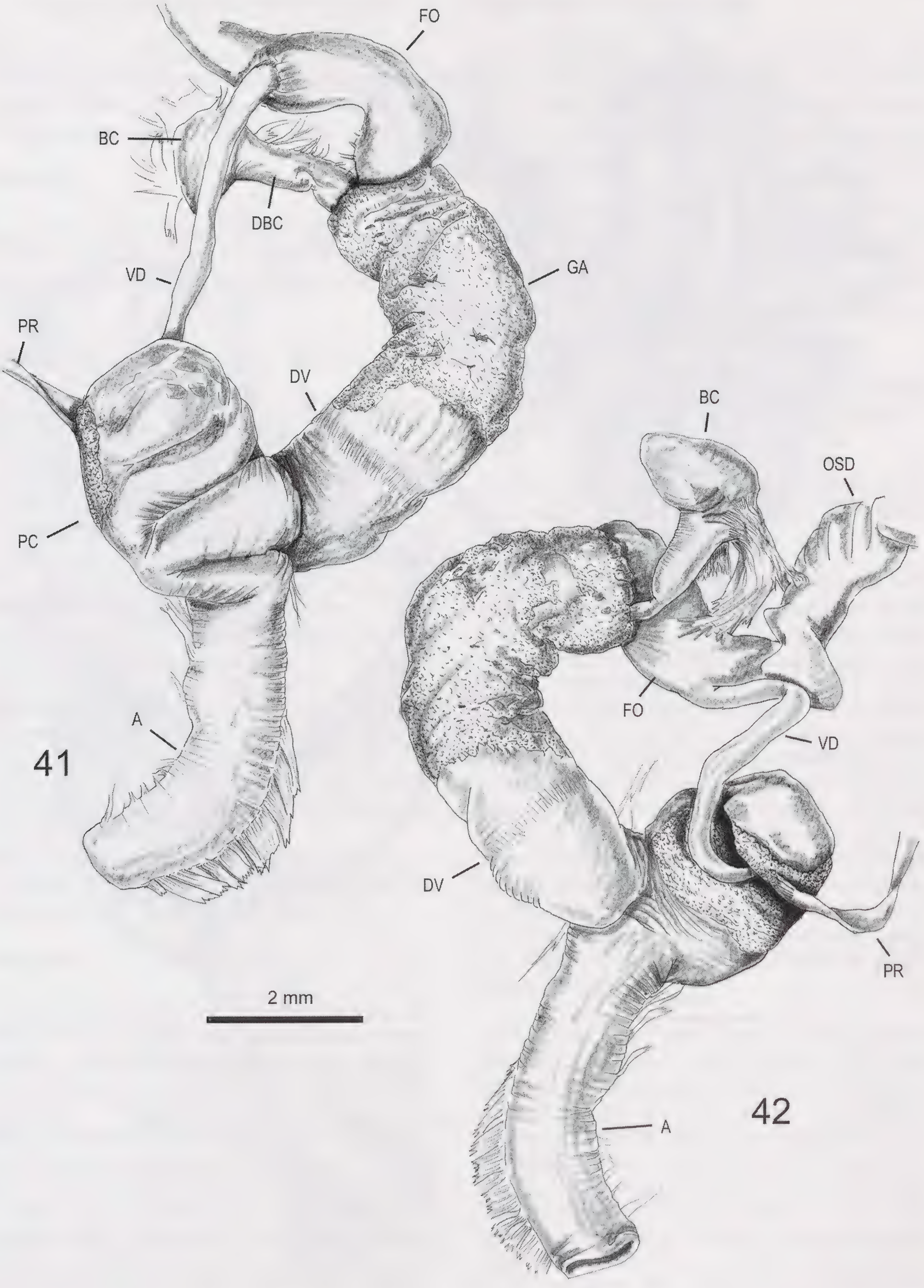


FIGS. 39, 40. *Madeirovitrina nitida* (Gould, 1847) from Ilha da Madeira, Pico Ruivo (Portugal), K. Groh leg. 7.1985. FIG. 39: Distal genitalia; FIG. 40: Internal structure of penial complex and vagina.

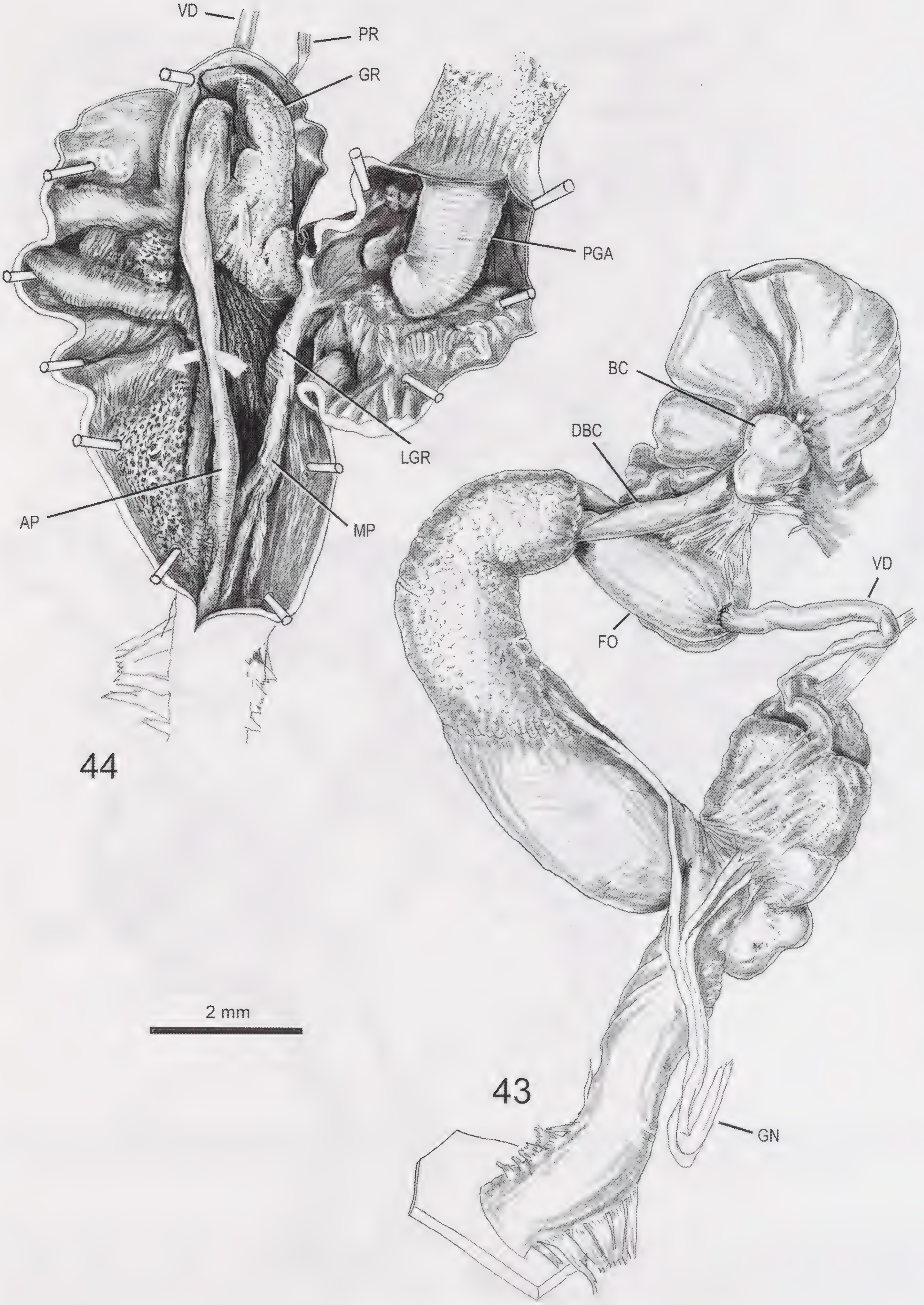
the distal penial complex and the vagina, near where the two enter the genital atrium.

The other *Madeirovitrina* species examined (*M. marcida*) differs from the type species in a number of characters (Figs. 41–44), but it shares a bridge-like accessory pilaster inside the penis.

All the analyses found that the two species of *Madeirovitrina* examined constitute a monophyletic group of Madeiran vitrinids supported by at least one exclusive synapomorphy, the bridge-like accessory pilaster (Figs. 14, 15; Table 3).



FIGS. 41, 42. Distal genitalia of a specimen of *Madeirovitrina marcida* (Gould, 1847) from Ilha da Madeira, Balcões (Portugal), K. Groh leg. 6.1989.



FIGS. 43, 44. *Madeirovitrina marcida* (Gould, 1847) from Ilha da Madeira, Balcões (Portugal), K. Groh leg. 6.1989. FIG. 43: Distal genitalia; FIG. 44: Internal structure of penial complex and vagina.

Oligolimax Fischer in: Paulucci, 1878

Type Species: *Vitrina (Oligolimax) paulucciae* Fischer in: Paulucci, 1878, by original designation. *Vitrina paulucciae* is a junior synonym of *Vitrina musignani* Pirajno, 1842.

Synonym

Gallandia Bourguignat, 1880. Type Species: *Vitrina conoidea* Martens, 1874, *sensu* Bourguignat, 1880, i.e., *G. olympica* Hausdorf, 1995.

Material Examined

Oligolimax annularis (Studer, 1820) – Italy: Alpi Apuane, Monte Pisanino, Valle Orto di Donna (Minucciano, Lucca), 32TNP9587, F. Giusti leg. 21.7.1970 (8 spirit specimens, FGC); Monte Terminillo (Rieti), 33TUH30, F. Giusti leg. 8.8.1966 (2 spirit specimens, FGC); Monti Sibillini, Val Canatra (Norcia, Perugia), 33TUH54, F. Giusti & G. Manganelli leg. 13.9.1988 (7 spirit specimens, FGC); Monte Pollino, Colle del Dragone (Morano Calabro, Cosenza), 33SWE9517, F. Giusti leg. 13.10.1977 (1 spirit specimen, FGC).

Oligolimax musignani (Pirajno, 1842) – Italy: Monti Nebrodi, Monte Soro, 1847 m (Cesarò, Messina), 33SVB7398, F. Giusti leg. 14.9.1981 (3 spirit specimens, FGC), G.B. Osella leg. 24.10.1981 (1 spirit specimen, FGC).

Oligolimax olympicus (Hausdorf, 1995) – Turkey: Orhangazi (Bursa), 35TPE98, B. Hausdorf leg. 25.9.1987 (1 shell, FGC).

Diagnosis

Snail-like vitrinids characterized by long penial retractor muscle arising from diaphragm, passing above right ommatophore retractor and ending on penial complex subapically; stimulator consisting of glandula amatoria with incomplete external glandular covering; penial complex with penial gland and without penial sheath; vas deferens contacting penial complex about medially, running inside its wall and entering it subapically; internal structures of penial complex comprising main and accessory pilaster; main pilaster consisting of large, medially pleated, proximal glandular roll and thin distal muscular pleat.

Description of Type Species

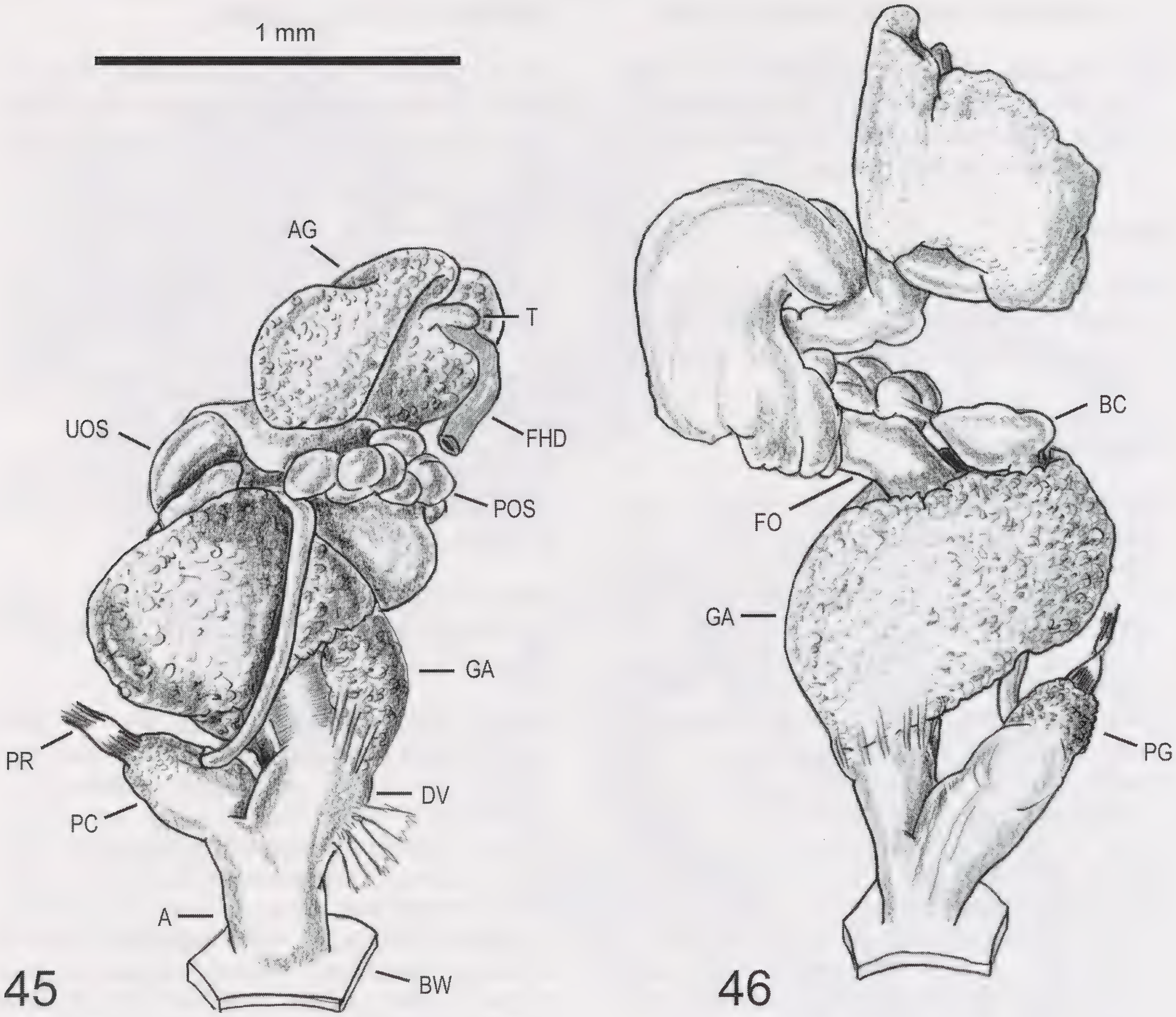
Shell: vitriniform typical, translucent, thin and fragile, globular-conical, sometimes angled with approximately 3.0 whorls; last whorl expanded; aperture moderately wide with columellar and basal margins bordered by narrow periostracal fringe; columellar margin normal; umbilicus open, punctiform; protoconch slightly prominent, with fine, wavy, irregularly branched, closely spaced, radial periostracal crests and isolated pits near suture; teleoconch with fine, closely and regularly spaced, slightly wavy, radial riblets (Manganelli & Giusti, 2004: figs. 1–7).

Body: can be withdrawn more or less completely into shell; right shell lobe absent (Manganelli & Giusti, 2004: fig. 9).

Radula: dichoglossan; marginal teeth partly pluricuspid (Manganelli & Giusti, 2004: 298–299, fig. 17).

Female Distal Genitalia (Figs. 45–48): free oviduct short and wide. Bursa copulatrix small and pyriform, with very short, slender duct, initially not flared. Vagina long, with large bulbous glandula amatoria constituting 1/2 to 2/3 of its length. Glandula amatoria with rather thin muscular wall, almost completely covered by external glandular layer; papilla of glandula amatoria very short. Internal surface of distal vagina rather smooth, with two longitudinal pilasters starting level with tip of papilla of glandula amatoria; larger pilaster rather robust, sometimes flanked by very thin pleats, originating from knob and ending by fusing with penial accessory pilaster; smaller pilaster very slender, ending by fusing with distal end of penial glandular roll.

Male Distal Genitalia (Figs. 45–48): penial complex very small and club-like, with penial gland and without penial sheath. Penial gland covering most of proximal penial complex. Penial retractor arising from diaphragm, long, inserted apically. Vas deferens medium in length, contacting penial complex about medially, then running inside thickness of penial gland and entering penial complex subapically near insertion of penial retractor. Internal structures of penial complex comprising main and accessory pilaster. Main pilaster consisting of large proximal glandular roll, divided into



FIGS. 45, 46. Distal genitalia of a specimen of *Oligolimax musignani* (Pirajno, 1842) from Monti Nebrodi, Monte Soro, 1847 m (Sicily, Italy), G. B. Osella leg. 24.10.1981.

initial yellow knoll, pale yellow medial portion and transversely pleated final portion (small dimensions prevent establishing homology with distal lamellate portion of glandular roll of other taxa) and thin distal muscular pleat fusing with lesser vaginal pleat. Accessory pilaster slender, arising on one side of glandular roll and ending by fusing on one side with pleat or system of pleats of genital atrium and, on other, with larger vaginal pleat. Vas deferens opening at top of distinct yellow knoll constituting initial part of glandular roll. Internal surface smooth.

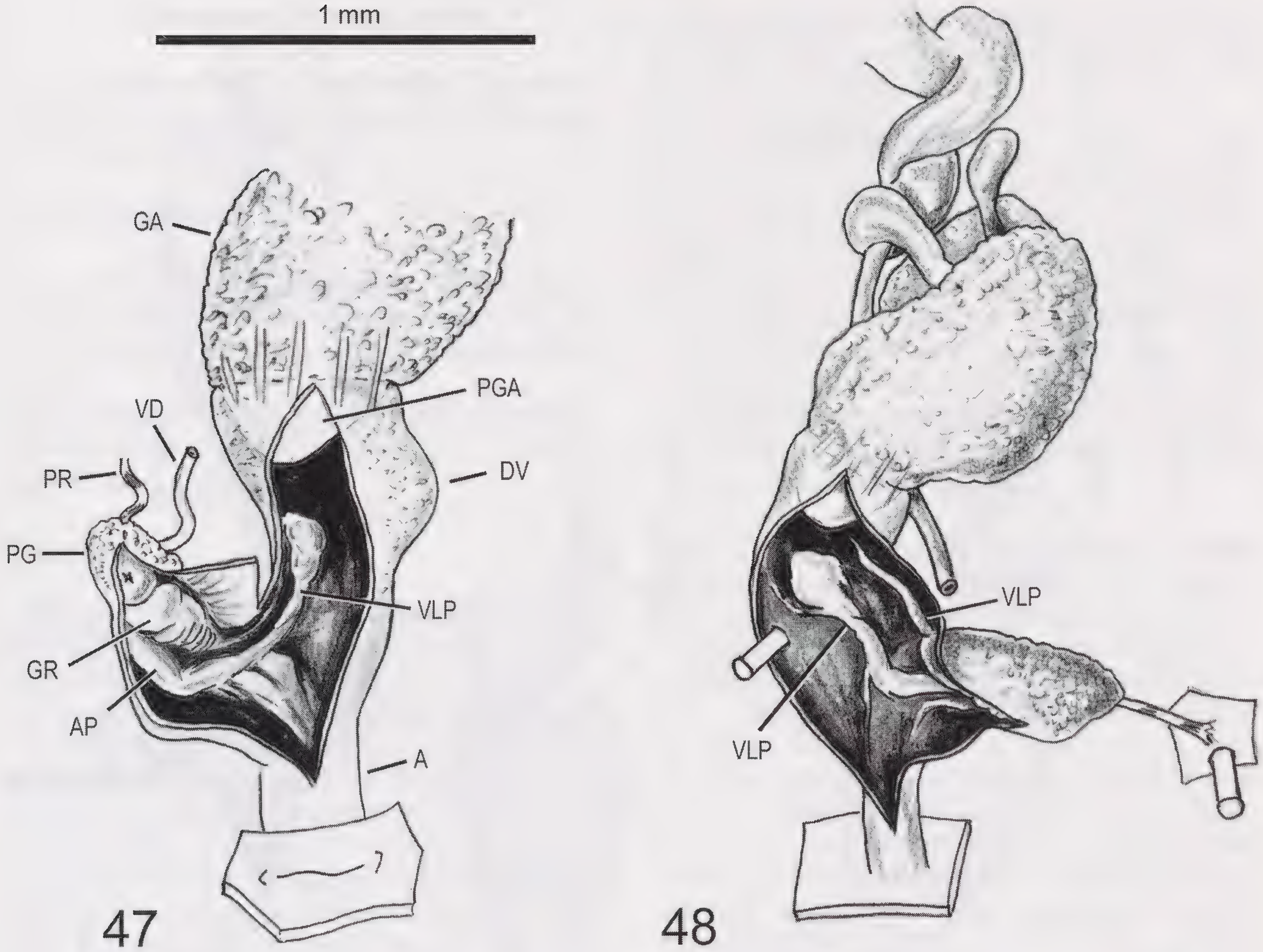
Genital Atrium (Figs. 45–48): short, with one side connected to body wall by robust muscular bands. Internal structures consisting of longitudinal pleat or system of pleats. Internal surface smooth.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: similar in juveniles and adults (Fig. 9). Penial retractor long, passing above right ommatophore retractor which is consequently free of penial complex and vagina.

Mating: no data available.

Remarks

Oligolimax was described by P. Fischer (in: Paulucci, 1878) as subgenus of *Vitrina* with two species originally included: *Vitrina paulucciae* Fischer in: Paulucci, 1878, and *Vitrina annularis* (Studer, 1820). It was subsequently regarded as a subgenus of *Phenacolimax* by Hesse (1923), Forcart (1957, 1959) and Zilch (1959), a section



FIGS. 47, 48. *Oligolimax musignani* (Pirajno, 1842) from Monti Nebrodi, Monte Soro, 1847 m (Sicily, Italy), F. Giusti leg. 14.9.1981. FIG. 47: Distal genitalia; FIG. 48: Internal structure of penial complex and vagina.

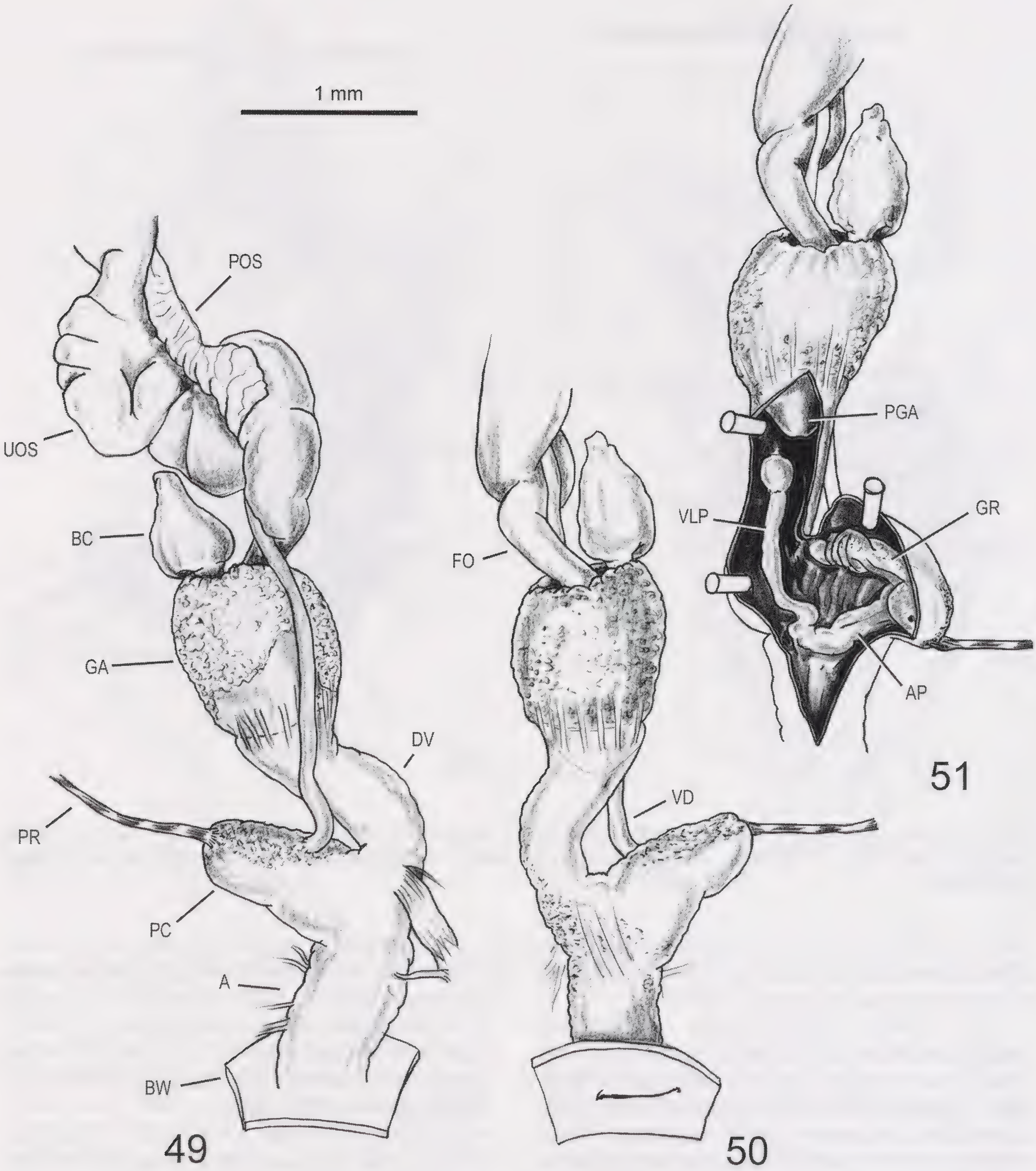
of subgenus *Vitrina* (s.s.) by Thiele (1931) and a distinct genus by Forcart (1944).

In the 1960s, Forcart (1965) claimed that the type-species was a junior synonym of *Vitrina bonelli* Targioni Tozzetti, 1873, and hence that *Oligolimax* had been used as a name for a completely different group of species, those hitherto included in *Semilimacella*, whereas the species hitherto included in *Oligolimax* had to be assigned to *Gallandia* Bourguignat, 1880 (type species: *Vitrina conoidea* Martens, 1874, *sensu* Bourguignat, 1880, i.e., *G. olympica* Hausdorf, 1995). *Gallandia* was subsequently regarded as a junior synonym of *Phenacolimax* by Schileyko (1986) and a distinct genus by Hausdorf (1995), Neubert (1998) and Alonso et al. (2000).

In a checklist of Italian malacofauna, Manganelli et al. (1995) reported that study of the syntypes of *V. paulucciae* demonstrated that Forcart (1965) was wrong to consider this species a junior synonym of *V. bonelli* and that *Oligolimax* was indeed available in the sense of Hesse (1924). Subsequently, Manganelli & Giusti (2004) demonstrated that *V. paulucciae* was in turn a junior synonym of *Vitrina musignani* Pirajno, 1842, and gave a complete redescription of the latter.

According to Hausdorf (2002), *Oligolimax* includes six species from the western Palaearctic (major anatomical references on which are: Forcart, 1959; Schileyko, 1986; Hausdorf, 1995, 2002; Manganelli & Giusti, 2004) and is the sister group of *Plutonia*; in turn, *Plutonia* and *Oligolimax* are the sister group of *Arabivitrina* and *Calidivitrina*.

Two out of the six species assigned to *Oligolimax* by Hausdorf (2002) belong to other genera (*O. lederi* to *Trochovitrina*; *O. pollonerianus* to *Sardovitrina*). Apart from *O. sturanyi*, the other species are well known anatomically (Hausdorf, 1995; Manganelli & Giusti, 2004). They have distal genitalia very similar in general scheme



FIGS. 49–51. *Oligolimax annularis* (Studer, 1820) from Monti Sibillini, Val Canatra (Umbria, Italy), F. Giusti & G. Manganelli leg. 13.9.1988. FIGS. 49, 50: Distal genitalia; FIG. 51: Internal structure of penial complex and vagina.

and internal structure, differing only in minor details (length of papilla of glandula amatoria, length of vagina, extension of glandular covering of glandula amatoria; see Manganelli & Giusti, 2004). Various nominal taxa of uncertain status were also assigned to this genus (cf. Manganelli & Giusti, 2004).

Most analyses find *Oligolimax* to be monophyletic, supported by non exclusive synapomorphies (Figs. 14, 15; Table 3); *Oligolimax* in turn constitutes a monophyletic group along with *Sardovitrina*, *Semilimacella* and *Vitrina*, based on the same relationships between the right ommatophore retractor and the distal genitalia.

Phenacolimax Stabile, 1859

Type Species: *Helicolimax major* Férussac, 1807, by subsequent designation (Fischer in: Paulucci, 1878).

Material Examined

Phenacolimax blanci (Pollonera, 1884) – Italy: Grotta della Melosa (Pigna, Imperia), G. Comotti leg. 2.8.1982 (4 spirit specimens, FGC).

Phenacolimax major (Férussac, 1807) – France: Mialet (Gard), M. Bodon leg. 1.12.1984 (2 spirit specimens, FGC).

Diagnosis

Semislug-like vitrinids characterized by short penial retractor muscle arising from diaphragm, compelling penial complex below right ommatophore and in front of right optic nerve and ending on penial complex subapically (but juveniles with long penial retractor muscle running in front of right optic nerve, below right ommatophore retractor); stimulator consisting of glandula amatoria with incomplete external glandular covering; penial complex with penial gland and penial sheath; vas deferens contacting penial complex medially, traversing penial sheath, running inside penial wall and entering it subapically; internal structures of penial complex comprising main pilaster, two accessory pilasters and tongue-like structure; main pilaster consisting of large, not clearly distally lamellate, proximal glandular roll and wrinkled distal muscular pleat.

Description of Type Species

Shell: vitriniform typical, glossy, thin and fragile, depressed, with approximately 2.5–3.0 whorls; last whorl expanded; aperture moderately wide with columellar and basal margins bordered by narrow periostracal fringe; columellar margin normal; umbilicus closed; protoconch not prominent, smooth, with many regular spiral rows of very small pits; teleoconch smooth (Kerney & Cameron, 1979: pl. 7, fig. 4a–c).

Body: cannot be withdrawn completely into shell; right shell lobe medium, covering limited portion of shell when animal undisturbed (Kerney & Cameron, 1979: pl. 7, fig. 4d; Falkner, 1992: figs. 11, 12 at p. 271).

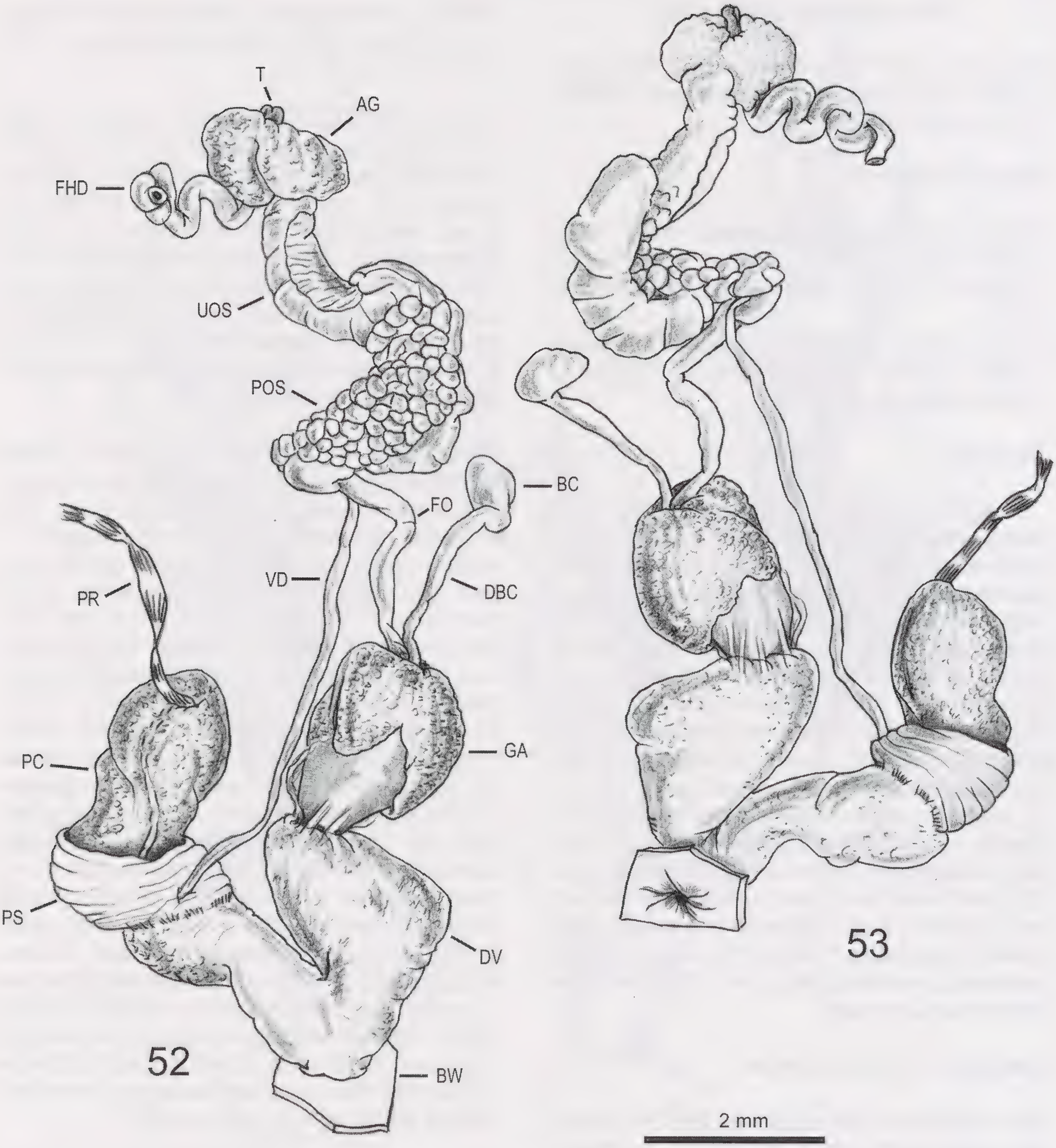
Radula: dichoglossan; marginal teeth bicuspid (with one small ectocone) (Hesse, 1923: 99–100, pl. 1, fig. 7).

Female Distal Genitalia (Figs. 52, 53, 55, 56): free oviduct long and slender. Bursa copulatrix small and oval to shoe-shaped, with short to medium (?), very slender duct, initially not flared. Vagina long, with small heart-like glandula amatoria constituting half its length. Glandula amatoria with very thick muscular wall, covered only proximally by external glandular layer; papilla of glandula amatoria very short. Internal surface of distal vagina with many thin, regular, transverse pleats.

Male Distal Genitalia (Figs. 52–54): penial complex large and club-like, with penial gland and penial sheath. Penial gland covering most of penial complex. Penial sheath medium in length, curled up, arising from mid penial complex and enveloping most of proximal penial complex. Penial retractor arising from diaphragm, short, inserted apically. Vas deferens long, contacting penial complex about medially, then traversing penial sheath, running inside thickness of penial gland and entering penial complex subapically near insertion of penial retractor. Internal structures of penial complex comprising main pilaster, two accessory pilasters and tongue-like structure. Main pilaster consisting of large proximal glandular roll, not clearly distally lamellate, and wrinkled distal muscular pleat ending in genital atrium side by side with two accessory pilasters. Accessory pilasters arising near tongue-like structure opposite glandular roll and ending in genital atrium. Vas deferens opening in transverse slit on glandular roll at about half its length. Internal surface with low irregularly arranged pleats and sparse spongy tissue with crypts.

Genital Atrium (Figs. 52–55): very short, without muscular bands. Internal structures consisting of distal portion of main and accessory pilasters. Internal surface as in penial complex.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: age-dependent (Figs. 3, 6). Juveniles with long slender penial retractor passing below right ommatophore and in front of right optic nerve; distal genitalia lying right of right ommatophore retractor which therefore appears free of penial complex and vagina. Adults with penial retractor short so



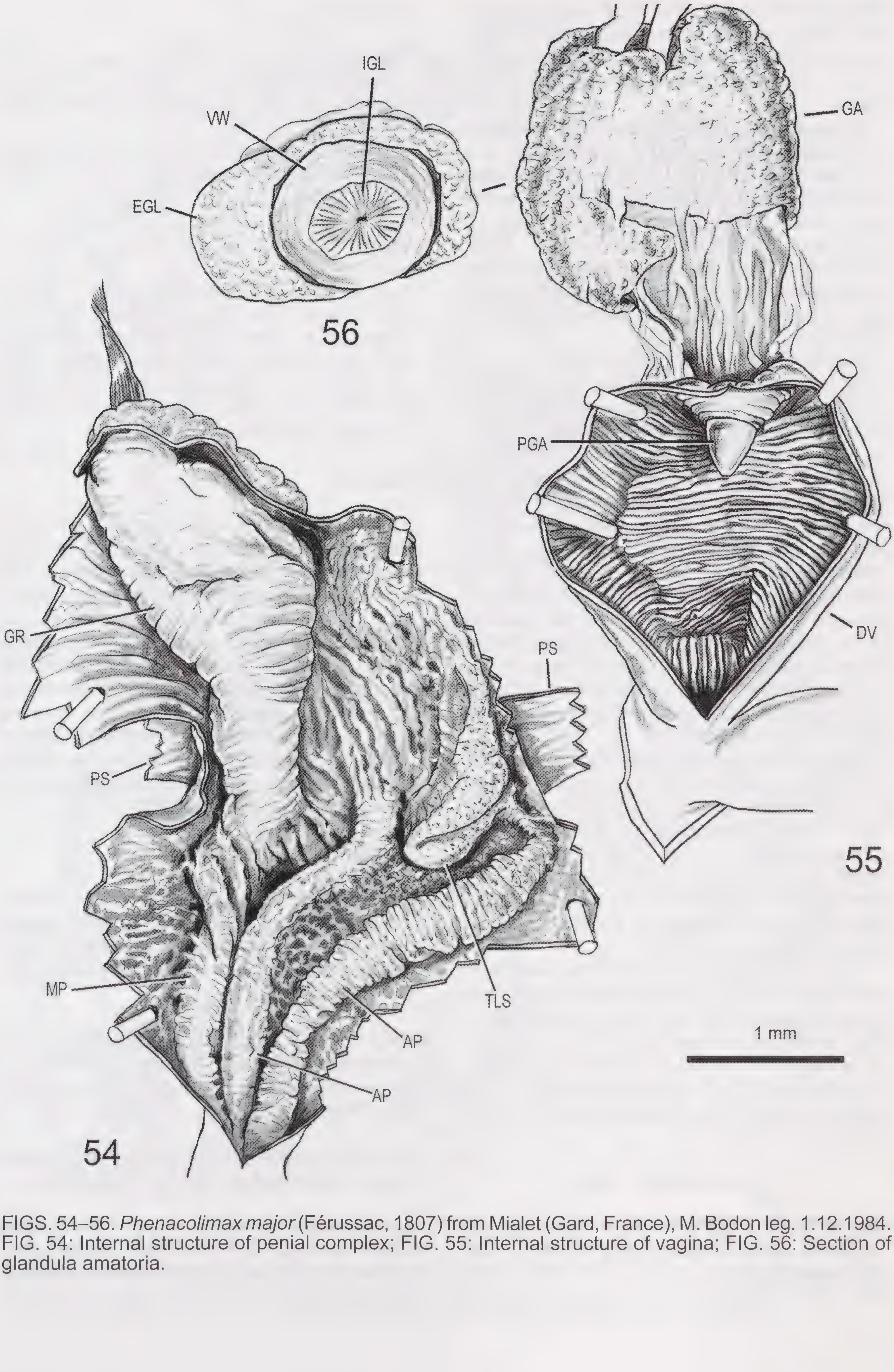
FIGS. 52, 53. Distal genitalia of a specimen of *Phenacolimax major* (Férussac, 1807) from Mialet (Gard, France), M. Bodon leg. 1.12.1984.

that entire penial complex is below right ommatophore and in front of right optic nerve; right ommatophore is consequently shifted right and compelled to lie between penial complex and vagina.

Mating: Hausdorf (2002) stated that stimulator is not used for fixing partner and penis is not inserted into vagina or duct of bursa copulatrix during copulation.

Remarks

Phenacolimax was established by Stabile (1859) with four species originally included. Overlooking the designation of *Helicolimax major* Férussac, 1807, as type species, Hesse (1923) considered *Phenacolimax* to belong to the "Gruppe der *V. pellucida* und *diaphana*". A few years later, Baker (1929) corrected Hesse's misinterpretation, restoring the correct



FIGS. 54–56. *Phenacolimax major* (Férussac, 1807) from Mialet (Gard, France), M. Bodon leg. 1.12.1984. FIG. 54: Internal structure of penial complex; FIG. 55: Internal structure of vagina; FIG. 56: Section of glandula amatoria.

sense of this taxon. *Phenacolimax* has since then been considered a distinct genus by all authors except Thiele (1931) and Hubendick (1953) who regarded it as a subgenus of *Vitrina*.

Although many species have been assigned to this genus in the course of time, only four species from western Europe are attributed now to *Phenacolimax* (Hausdorf, 2002; Gavetti et al., 2008) (major anatomical references on which are: Forcart, 1949; Boato et al., 1986; De Winter, 1990; Neubert, 1998). According to Hausdorf (2002), *Phenacolimax* is the sister group of ((*Arabivitrina*, *Calidivitrina*) (*Plutonia*, *Oligolimax*)).

Moquin Tandon (1855, 2: 49–52, Atlas: pl. 6, figs. 14–32) gave a detailed but incorrect description of the male distal genitalia of *P. major*. According to him, the penial complex had a very large, long proximal part bent on itself and referred to as "flagellum épais". Actually, Moquin Tandon was unable to see that the vas deferens only contacted the penis at about half of the penis length, traversed the penial sheath, ran inside the penial gland and ended near the penis apex. Moquin Tandon's description and figure probably inspired the scheme of the distal genitalia of *P. major* published by Germain (1930: fig. 89), since it reproduces a penial complex with vas deferens entering penis at half its length and with a long flagellum twisted in the shape of an "S".

Phenacolimax species differ by virtue of genital atrium length (short vs. long), point of origin of penial sheath (distal vs. medial) and other minor details. *Phenacolimax* shares the same age-dependent relationships between right ommatophore retractor and distal genitalia with *Arabivitrina*, but is distinct by virtue of a penial sheath and the absence of a distal lamellate portion of the glandular roll.

There is no evidence that *Phenacolimax* species constitute a monophyletic group. Suspecting a relationship between *Eucobresia* and *Phenacolimax*, we investigated this hypothesis by phylogenetic analysis of three species of *Eucobresia* and two of *Phenacolimax*, but no clade including these species, or at least some of them, was recovered.

Plutonia Stabile, 1864

New name for *Viquesnelia* Morelet, 1860 (type species *Viquesnelia atlantica* Morelet, 1860, by monotypy).

Synonyms

Viquesnelia Morelet, 1860. Type Species: *Viquesnelia atlantica* Morelet, 1860, by monotypy. *Non Viquesnelia* Deshayes, 1857

Vitriplutonia Collinge, 1893, new name for *Plutonia* Stabile, 1864 (according to Bank et al., 2002).

Material Examined

Plutonia atlantica (Morelet, 1860) – Portugal: Ilha de São Miguel (Azores), Serra de Tronqueira, T. Backeljau leg. 28.6.1989 and 6.6.1990 (5 spirit specimens, IRSNB); Pico do Carvão, T. Backeljau leg. 16.7.1989, 8.6.1990, 26.6.1989, 16.7.1989 and 3.7.1989 (22 spirit specimens, IRSNB).

Diagnosis

Slug-like vitrinids characterized by short modified penial retractor (consisting of three branches, none reaching penial complex: first reaches bursa copulatrix and its duct, second reaches free oviduct and third reaches vas deferens); stimulator consisting of glandula amatoria with complete external glandular covering; penial complex with penial gland and without penial sheath; vas deferens entering penial complex apically; internal structures of penial complex comprising main and accessory pilasters (?); main pilaster comprising large, not distally lamellate glandular roll.

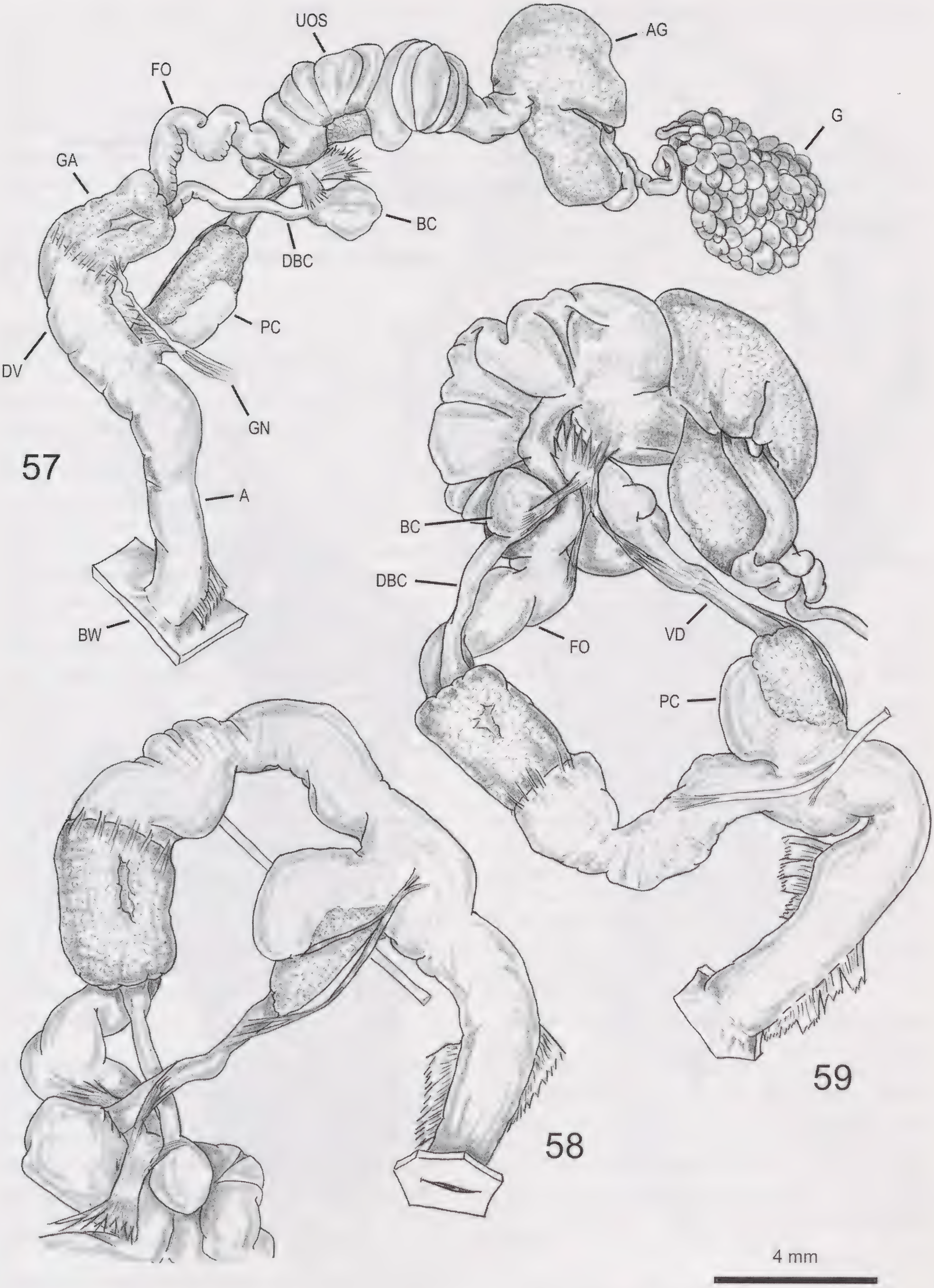
Description of Type Species

Shell: internal, limacella-like, rather thin, convex and with traces of growth lines above, slightly concave below, with nucleus (protoconch area) lying over sort of basal tab (Wiktor & Backeljau, 1995: figs. 5–10).

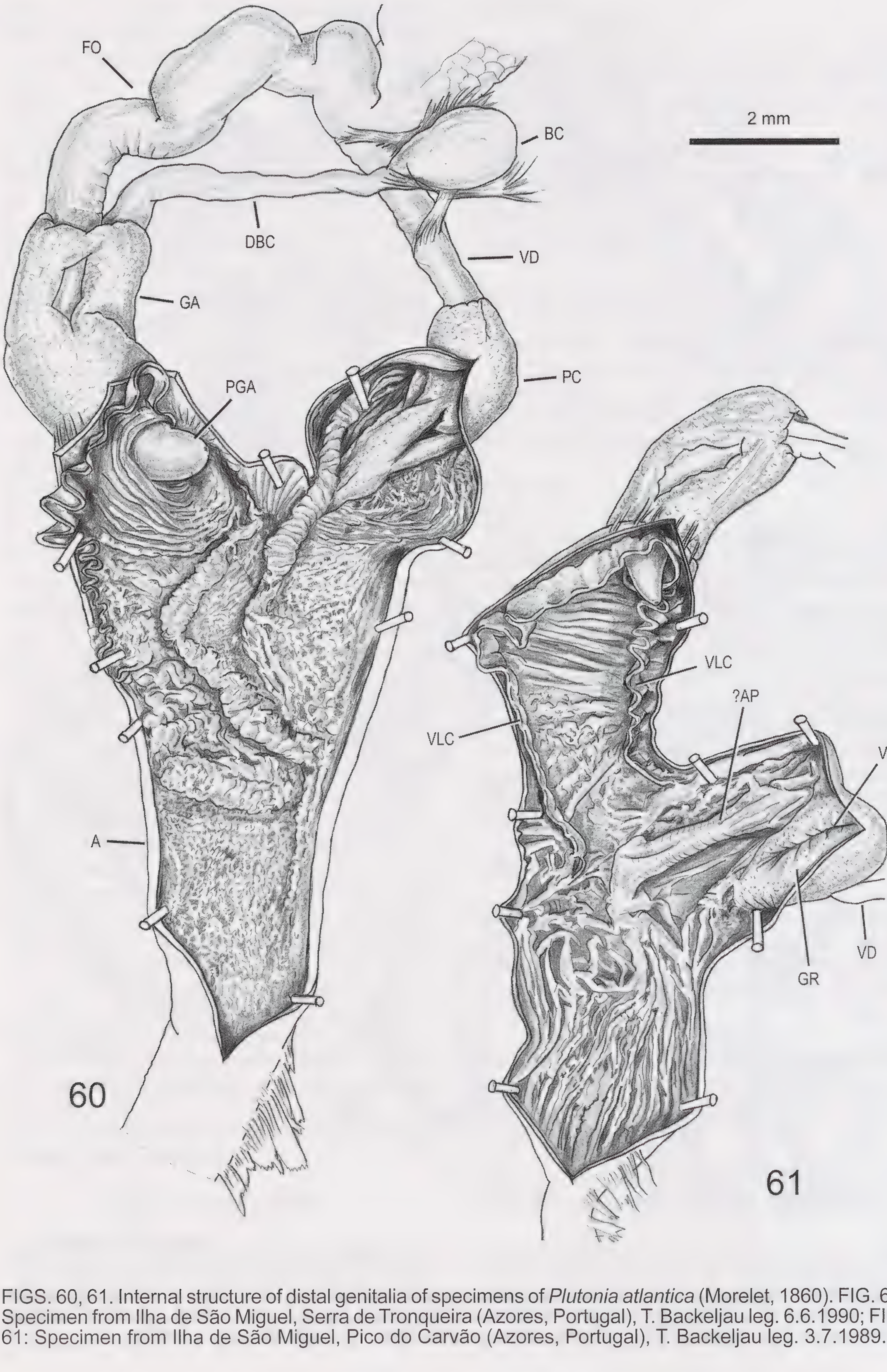
Body: slug-like having large oval clypeus with postmedian pneumostome and tail laterally compressed with evident continuous dorsal keel (Wiktor & Backeljau, 1995: figs. 1–4).

Radula: beloglossan; all teeth monocuspid (Wiktor & Backeljau, 1995: 75, figs. 22–25).

Female Distal Genitalia (Figs. 57–61): free oviduct short to long and wide. Bursa copulatrix small and oval, with short to medium,



FIGS. 57–59. Distal genitalia of *Plutonia atlantica* (Morelet, 1860). FIG. 57: Specimen from Ilha de São Miguel, Serra de Tronqueira (Azores, Portugal), T. Backeljau leg. 6.6.1990; FIGS. 58, 59: Specimen from Ilha de São Miguel, Pico do Carvão (Azores, Portugal), T. Backeljau leg. 3.7.1989.



FIGS. 60, 61. Internal structure of distal genitalia of specimens of *Plutonia atlantica* (Morelet, 1860). FIG. 60: Specimen from Ilha de São Miguel, Serra de Tronqueira (Azores, Portugal), T. Backeljau leg. 6.6.1990; FIG. 61: Specimen from Ilha de São Miguel, Pico do Carvão (Azores, Portugal), T. Backeljau leg. 3.7.1989.

more or less slender duct, initially not flared. Vagina long, with small cylindrical glandula amatoria constituting 1/2 to 2/3 of its length. Glandula amatoria with thick muscular wall, almost completely covered by external glandular layer; papilla of glandula amatoria short. Internal surface of distal vagina with thin, mainly transverse pleats and two longitudinal wavy laminar crests (one larger and longer and the other sometimes less evident) starting from base of papilla of glandula amatoria and ending before genital atrium.

Male Distal Genitalia (Figs. 57–61): penial complex small and nearly bilobate, with penial gland and without penial sheath. Penial gland covering one side of penial complex. Penial retractor arising from diaphragm, short modified and divided into three branches, none of which reaches penial complex: first reaches bursa copulatrix and its duct, second free oviduct and third vas deferens (sometimes thin muscular branches connect distal vas deferens and penial complex). Vas deferens short and thick, entering penial complex apically. Internal structures of penial complex comprising main and accessory pilasters. Main pilaster consisting of large glandular roll, not distally lamellate. Accessory pilaster more or less superficially pleated, arising near proximal glandular roll and ending in proximal genital atrium. Vas deferens opening inside long longitudinal groove on glandular roll (in an adult specimen examined, sort of small tongue-like structure projected over groove of glandular roll). Internal surface with low, irregularly arranged pleats.

Genital Atrium (Figs. 57–61): very long and cylindrical, with opposite sides connected to body wall by robust muscular bands. Internal surface with thin mainly longitudinal pleats or spongy tissue.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: due to the fact that penial retractor is modified and divided into three branches, none of which reaches penial complex, right ommatophore retractor is free of distal genitalia (in juveniles of a single population right ommatophore retractor was found both below and above penial complex).

Mating: no data available. Hausdorf (2002) stated that in *Plutonia* penis is not inserted into vagina or duct of bursa copulatrix during copulation. However this observation is not based on *P. atlantica* but on some other species he included in this genus.

Remarks

Plutonia was introduced by Stabile (1864) as a new name for *Viquesnelia* Morelet, 1860, a genus established for a slug-like vitrinid of the Azores, *Viquesnelia atlantica*, which turned out to be a junior homonym of *Viquesnelia* Deshayes, 1857.

Simroth (1891) claimed that *Plutonia* was related to other Macaronesian vitrinids and this was accepted by all subsequent authors, except Wiktor & Backeljau (1995), who supported its inclusion in a distinct family (Plutoniidae). *Plutonia* has been regarded as a distinct monospecific genus by Simroth (1891), Thiele (1931) and Schileyko (1986), a subgenus of *Phenacolimax* by Forcart (1957), Zilch (1959) and Backhuys (1975), a genus divided into five subgenera including all Macaronesian vitrinds by Alonso et al. (2000) and Hausdorf (2002) and a genus divided into two subgenera (*Plutonia* s.s. and *Canarivitrina*) by Schileyko (2003).

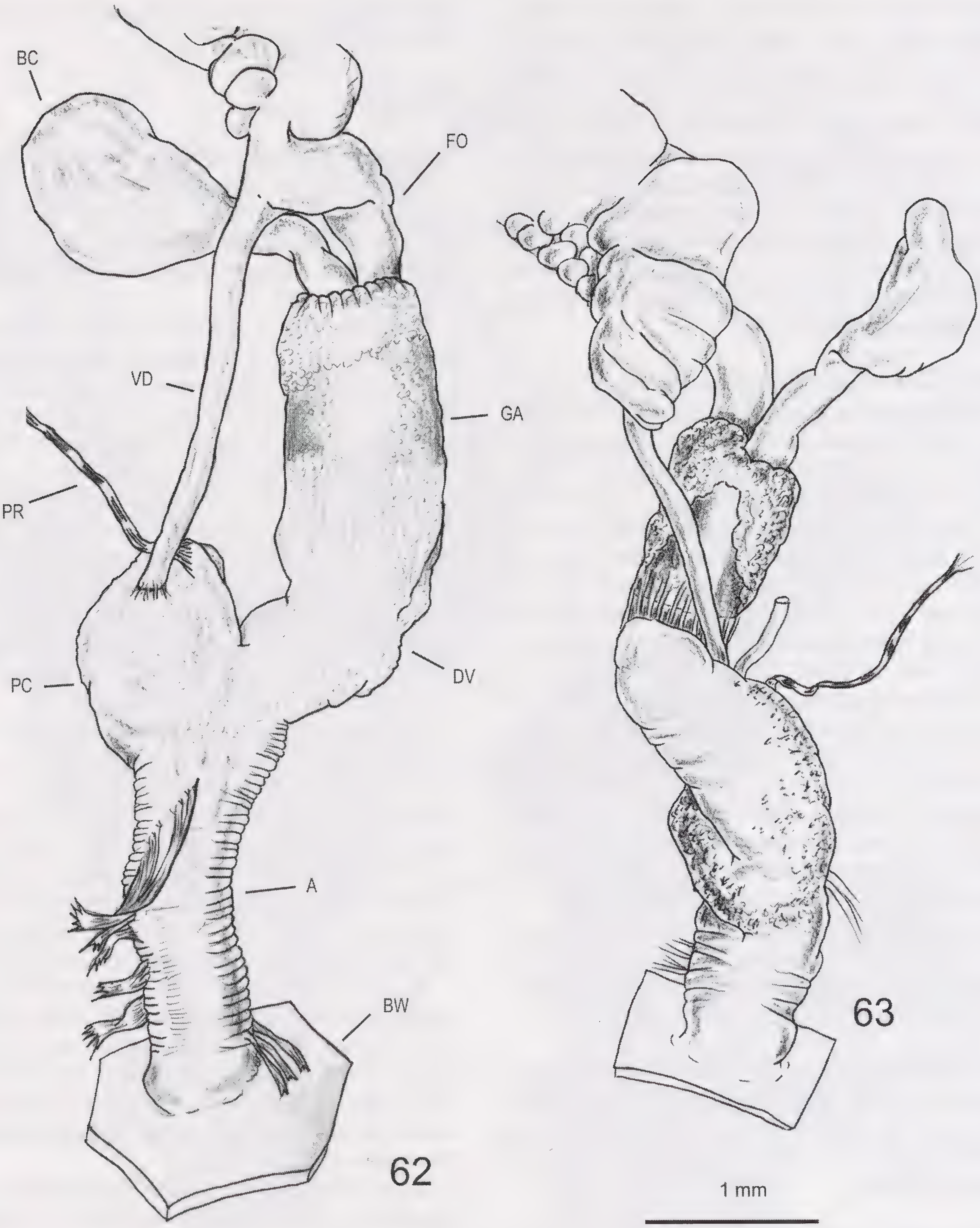
Plutonia includes only the type species, *P. atlantica* (major anatomical references on which are: Simroth, 1891; Wiktor & Backeljau, 1995) although it may constitute a group of cryptic species (Medeiros et al., 2000). According to Hausdorf (2002), *Plutonia* (as including all Macaronesian vitrinds) is the sister group of *Oligolimax*; in turn *Plutonia* and *Oligolimax* are the sister group of *Arabivitrina* and *Calidivitrina*.

Study of many specimens from different localities showed remarkable difference in shape and internal ornamentation of the various parts of the distal genitalia (compare Figs. 57–61). This might suggest the existence of more than one species of *Plutonia*, as hypothesized by Medeiros et al. (2000).

Some other Azorean semislug vitrinids, assigned to *Azorivitrina* (*A. brumalis*, *A. finitima* and *A. laxata*), share the same scheme of the distal genitalia (long to very long free oviduct, vagina and genital atrium; short to very short penial complex) with *Plutonia atlantica* (cf. Figs. 19–22; see also Mordan & Martins, 2001). However, phylogenetic analysis does not recover any monophyletic group including *Plutonia atlantica* and *Azorivitrina* species.

Sardovitrina Manganelli & Giusti, 2005

Type Species: *Vitrina polloneriana* [Arbanasich], 1897, by original designation.



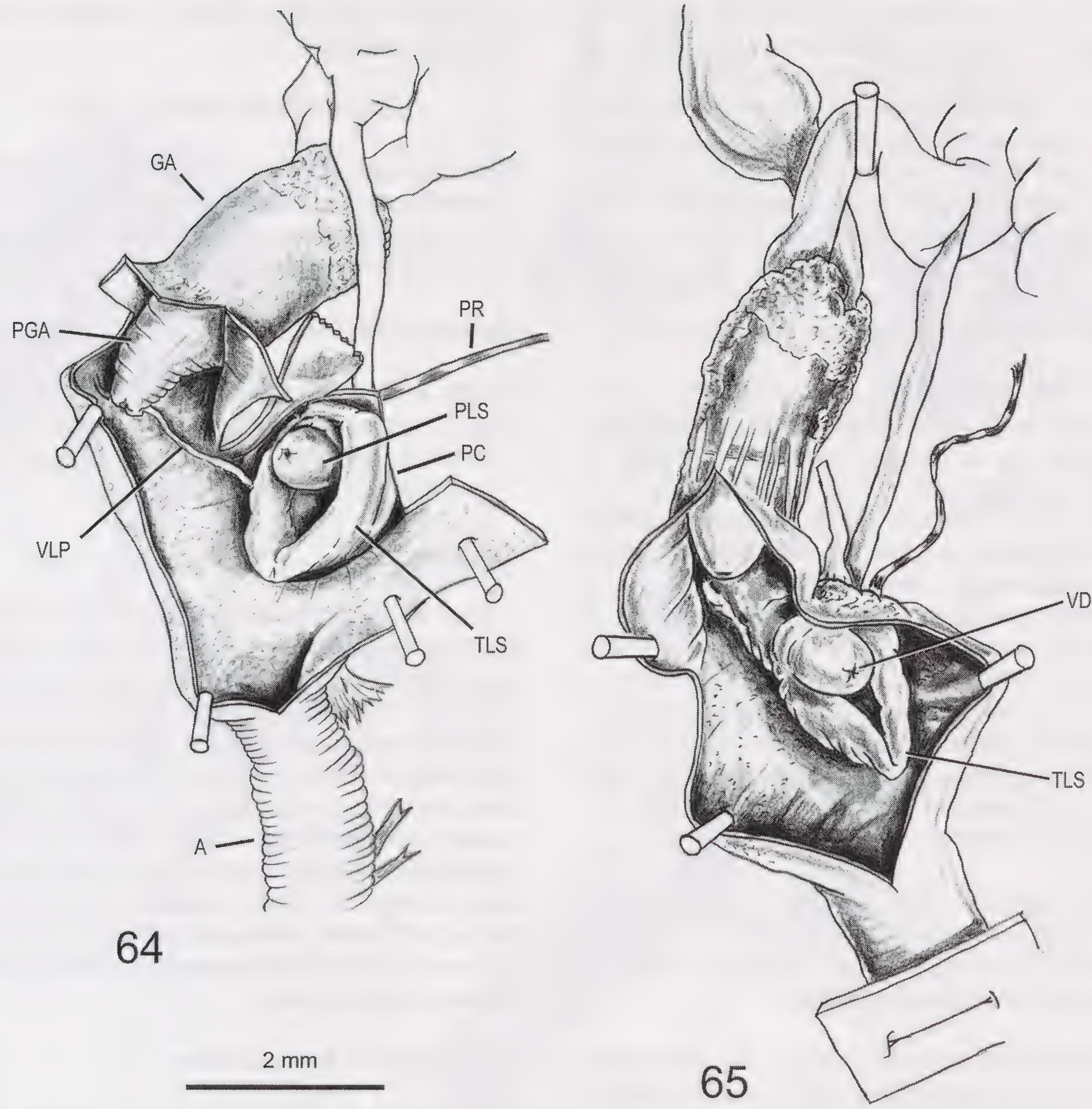
FIGS. 62, 63. Distal genitalia of specimens of *Sardovitrina polloneriana* ([Arbanasich], 1897). FIG. 62: Specimen from Lanusei (Sardinia, Italy), J. A. J. Nienhuis leg. 25.1.1972; FIG. 63: Specimen from Arbatax (Sardinia, Italy), J. A. J. Nienhuis leg.

Material Examined

Sardovitrina polloneriana ([Arbanasich], 1897) – Italy: Arbatax (Tortolì, Nuoro), 32SNK62, J. A. J. Nienhuis leg. (7 spirit specimens, FGC); Lanusei (Lanusei, Nuoro), 32TNK41, J. A. J. Nienhuis leg. 25.1.1972 (10 spirit specimens, FGC).

Diagnosis

Semislug-like vitrinids characterized by long penial retractor muscle arising from diaphragm, passing above right ommatophore retractor and ending on penial complex apically; stimulator consisting of glandula amatoria; penial complex very small with penial gland and without penial



FIGS. 64, 65. Internal structure of penial complex and vagina of specimens of *Sardovitrina polloneriana* ([Arbanasich], 1897). FIG. 64: Specimen from Lanusei (Sardinia, Italy), J. A. J. Nienhuis leg. 25.1.1972; FIG. 65: Specimen from Arbatax (Sardinia, Italy), J. A. J. Nienhuis leg.

sheath; vas deferens entering penial complex subapically; internal structures of penial complex distinctive and consequently difficult to homologize, comprising short, rolled, tongue-like structure embracing distinct, cylindrical, papilla-like structure.

Description of Type Species

Shell: vitriniform typical, glossy, thin and fragile, depressed, with approximately 3.0 whorls, last whorl expanded; aperture moderately wide with columellar and basal margins bordered by narrow periostracal fringe; columellar margin normal; umbilicus open, punctiform; protoconch slightly prominent with blunt, closely spaced, radial ribs and very small pits; teleoconch smooth (Manganelli & Giusti, 2005: figs. 1–6).

Body: cannot be completely withdrawn into shell; right shell lobe medium, covering limited portion of shell when animal undisturbed (Manganelli & Giusti, 2005: fig. 7).

Radula: dichoglossan; marginal teeth pluricuspid (Manganelli & Giusti, 2005: 574–575, figs. 16–18).

Female Distal Genitalia (Figs. 62–65): free oviduct short and wide. Bursa copulatrix medium in size and sac-like, with short, slender duct, initially not flared. Vagina long, with small cylindrical glandula amatoria constituting half its length. Glandula amatoria with very thick muscular wall, covered only proximally by external glandular layer; papilla of glandula amatoria short. Internal surface of distal vagina rather smooth, with spongy glandular tissue and one very thin pleat starting level with tip of papilla of glandula amatoria and ending by fusing with base of penial rolled tongue-like structure.

Male Distal Genitalia (Figs. 62–65): penial complex very small and globular (sometimes so short as to appear simple outgrowth of distal vagina), with penial gland and without penial sheath. Penial gland covering sparsely most of penial complex. Penial retractor arising from diaphragm, long, inserted apically. Vas deferens medium in length, entering penial complex subapically near insertion of penial retractor. Internal structures of penial complex distinctive and therefore difficult to homologize, comprising short, rolled tongue-like structure embracing distinct, cylindrical papilla-like structure. Vas deferens opening at tip of papilla-like structure. Internal surface smooth.

Genital Atrium (Figs. 62–65): very long and cylindrical, with one side connected to body wall by robust muscular bands. Internal surface as in vagina and penial complex.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: similar in juveniles and adults (Fig. 9). Penial retractor long, passing above right ommatophore retractor which is consequently free of penial complex and vagina.

Mating: no data available.

Remarks

Sardovitrina is a monotypic genus, recently described by Manganelli & Giusti (2005) for a species from Sardinia (western Mediterranean) having a scheme of the distal genitalia (long to very long free oviduct, vagina and genital atrium; short to very short penial complex) reminescent of some Macaronesian vitrinids (*Plutonia atlantica* and some species of *Madeirovitrina* and *Azorivitrina*) and sharing the same relationships between the right ommatophore retractor and the distal genitalia with species of *Oligolimax*, *Semilimacella* and *Vitrina.* Indeed, MP and AP showed that *Sardovitrina* constitutes a monophyletic group with these genera, supported by an exclusive synapomorphy, namely the course of the penial retractor.

Trochovitrina Boettger, 1880

Type Species: *Vitrina (Trochovitrina) subcarinata* Boettger, 1880, by monotypy. *Vitrina subcarinata* is a junior synonym of *Lampadia lederi* Boettger, 1878.

Material Examined

Trochovitrina lederi (Boettger, 1878) – Azerbaijan: "Lenkoran lowland and Talysh Mountains", A. A. Schileyko leg. 24.3.1965 (2 spirit specimens, ZMMU Lc-19985).

Diagnosis

Snail-like vitrinids characterized by penial retractor muscle arising from diaphragm and ending on penial complex apically (path unknown); stimulator consisting of glandula amatoria with complete external glandular covering (papilla of glandula amatoria apparently missing); penial complex with penial gland and without penial sheath; vas deferens entering penial complex proximally; internal structures of penial complex comprising only main pilaster, consisting of large, not distally lamellate, proximal glandular roll and robust distal muscular pleat, ending before genital atrium.

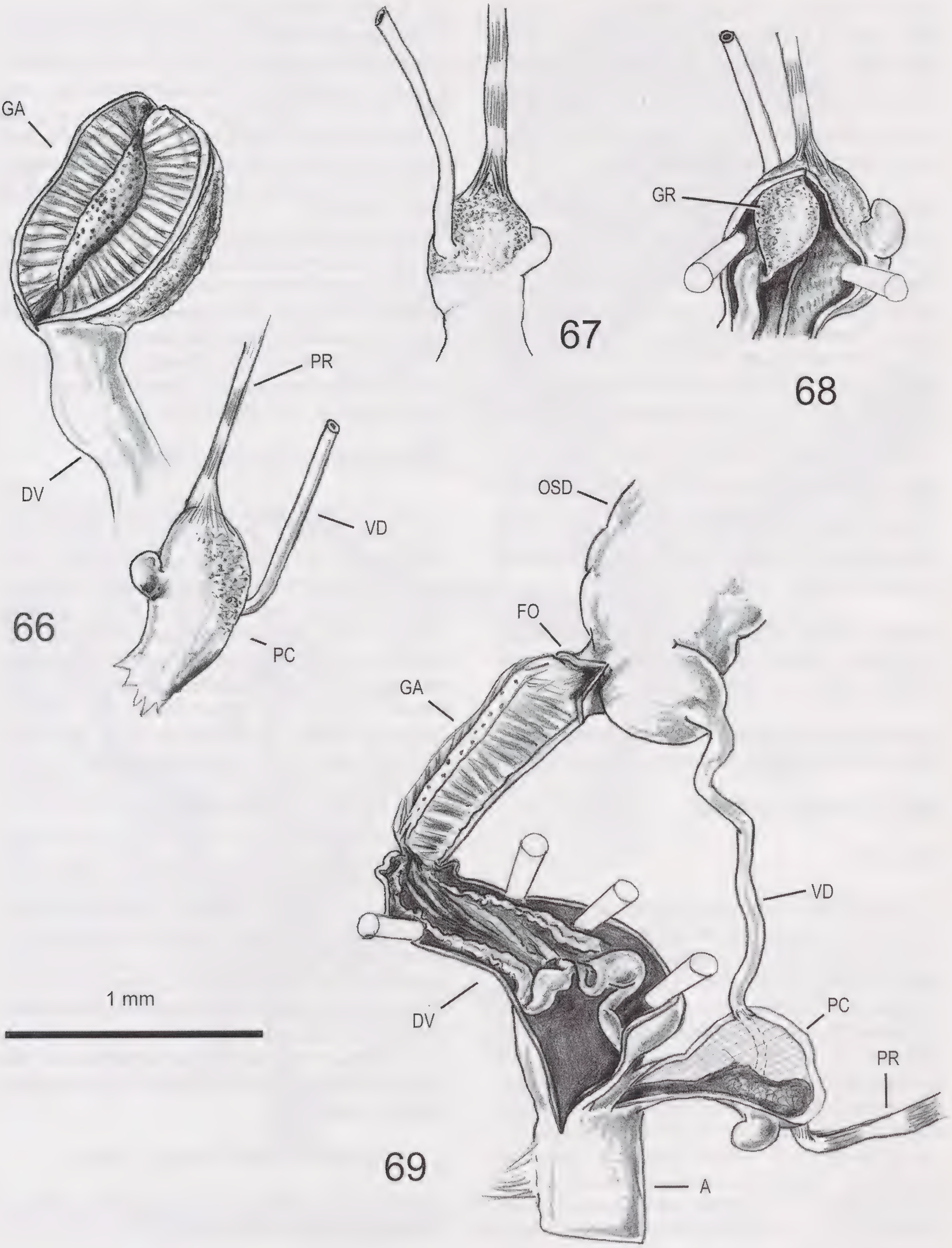
Description of Type Species

Shell: trochiform, translucent, thin and fragile, conical-depressed, sharply angled, with approximately 3.0 whorls; last whorl expanded; aperture moderately wide with margin not bordered by periostracal fringe; columellar margin normal; umbilicus open, punctiform; protoconch prominent, with fine, closely spaced, radial riblets and no evidence of pitting; teleoconch with fine, closely and regularly spaced, slightly wavy, radial riblets (Schileyko, 2003: fig. 1908A).

Body: no data available; it may possibly be withdrawn completely into shell, since shell lobes are probably very small (Hausdorf, 1995: 71).

Radula: dichoglossan; marginal teeth partly pluricuspid (Hausdorf, 1995: table 1).

Female Distal Genitalia (Figs. 66, 69): free oviduct short and wide. Bursa copulatrix and its duct apparently absent. Vagina long, with large bulbous glandula amatoria constituting half its



FIGS. 66–69. *Trochovitrina lederi* (Boettger, 1878) from "Lenkoran lowland and Talysh Mountains" (Azerbaijan), A. A. Schileyko leg. 24.3.1965. FIG. 66: Partial distal genitalia; FIG. 67: Detail of penial complex; FIG. 68: Internal structure of penial complex; FIG. 69: Internal structure of female distal genitalia and section of penial complex.

length. Glandula amatoria with thin muscular wall, almost completely covered by external glandular layer; papilla of glandula amatoria absent (?). Internal surface of distal vagina with mainly longitudinal pleats, two of which longer, more evident and wavy, ending near genital atrium as raised and rolled crests.

Male Distal Genitalia (Figs. 66–69): penial complex small and club-like, with small knob-like diverticulum at about half its length, with penial gland and without penial sheath. Penial gland covering side of proximal penial complex facing vagina. Penial retractor arising from diaphragm, long, inserted apically. Vas deferens medium in length, entering penial complex proximally, thus dividing it into short pointed flagellum and penis proper. Internal structures of penial complex comprising main pilaster only which consists of large proximal glandular roll, not distally lamellate, and robust distal muscular pleat, ending before genital atrium. Vas deferens opening on glandular roll at about half its length. Internal surface smooth.

Genital Atrium (Fig. 69): long with one side connected to body wall by thin muscular bands. Internal surface smooth.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: unknown.

Mating: no data available.

Remarks

Trochovitrina was established by Boettger (1880) as a subgenus of *Vitrina*. Later it was considered a junior synonym of *Gallandia* by Baker (1929), Thiele (1931) and Zilch (1959).

Schileyko (1986) resurrected it as a valid monospecific genus characterized by very short free oviduct, absence of bursa copulatrix and its duct, structure of wall of glandula amatoria, absence of papilla of glandula amatoria and penial complex with small subapical tubercle.

In a revision of Turkish vitrinids, Hausdorf (1995) did cladistic analysis to elucidate the relationships of *T. lederi* with *Gallandia annularis* and *G. paulucciae* using *Insulivitrina* as outgroup. He found that these three taxa constitute a monophyletic group (*G. annularis* (*G. olympica*, *T. lederi*)) and consequently regarded *Trochovitrina* as a junior synonym of *Gallandia* (*Gallandia* is a junior synonym of *Oligolimax*).

Our anatomical study on the specimen already studied by Schileyko (1986: 130–131, fig. 4; 2003: 1479, fig. 1908) (and consequently highly fragmented) has largely confirmed his anatomical description, particularly the absence of bursa copulatrix and papilla of glandula amatoria. A few details must be added: presence of penial gland on one side of proximal penial complex; presence of a main pilaster consisting of a proximal glandular roll and a robust distal muscular pleat.

Anatomical study of other specimens is needed to detect important features such as relationships between penial retractor and right ommatophore retractor and to confirm absence of bursa copulatrix and papilla of glandula amatoria.

Pending more detailed investigation we leave *Trochovitrina* as a distinct genus (instead of a junior synonym of *Oligolimax*).

Vitrinids with Diverticular Stimulator

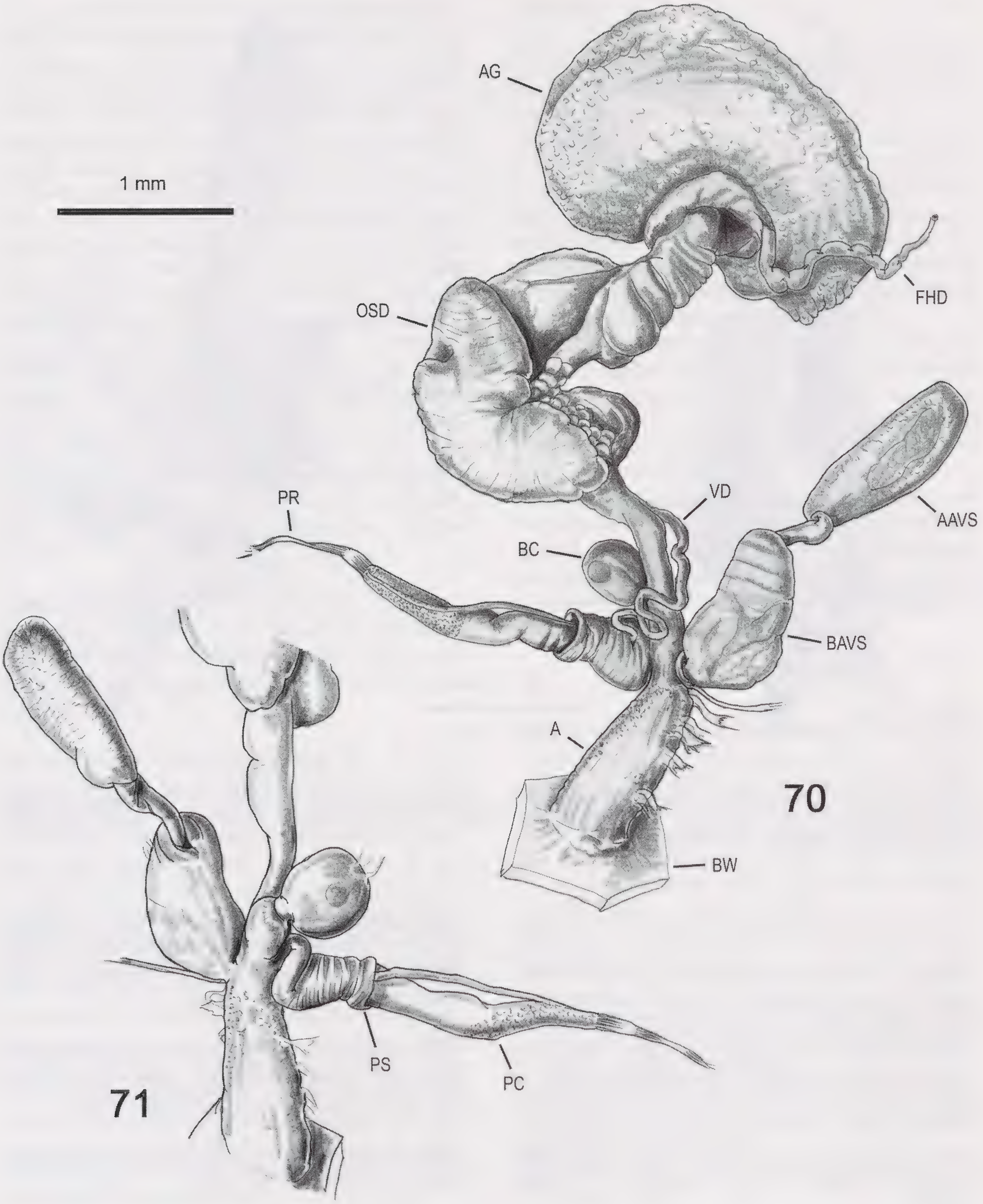
The vitrinids with diverticular stimulator include four taxa of the genus group (*Hessemilimax*, *Semilimacella*, *Semilimax* and *Vitrinobrachium*). Our phylogenetic analyses suggested that they belong to three different lineages with unresolved basal relationships: the first was *Vitrinobrachium*, the second *Hessemilimax* and *Semilimax* and the third *Semilimacella* and other taxa. The *Vitrinobrachium* clade was present in all analyses and was one of the most supported by MP. The clade including *Hessemilimax* and the three species of *Semilimax* was present in some analyses; the relationships between its members were not resolved, though MP supported a subclade consisting of *Semilimax pyrenaicus* and *S. semilimax*. The relationships of *Semilimacella* were more controversial: the two species might constitute a monophyletic (see BI) or paraphyletic group belonging to a larger monophyletic group including other taxa (species of *Oligolimax*, *Sardovitrina* and *Vitrina*) on the basis of the exclusive disposition of the penial retractor above the right ommatophore retractor (see AP).

Hessemilimax Schileyko, 1986

Type Species: *Vitrina kotulae* Westerlund, 1883, by original designation.

Material Examined

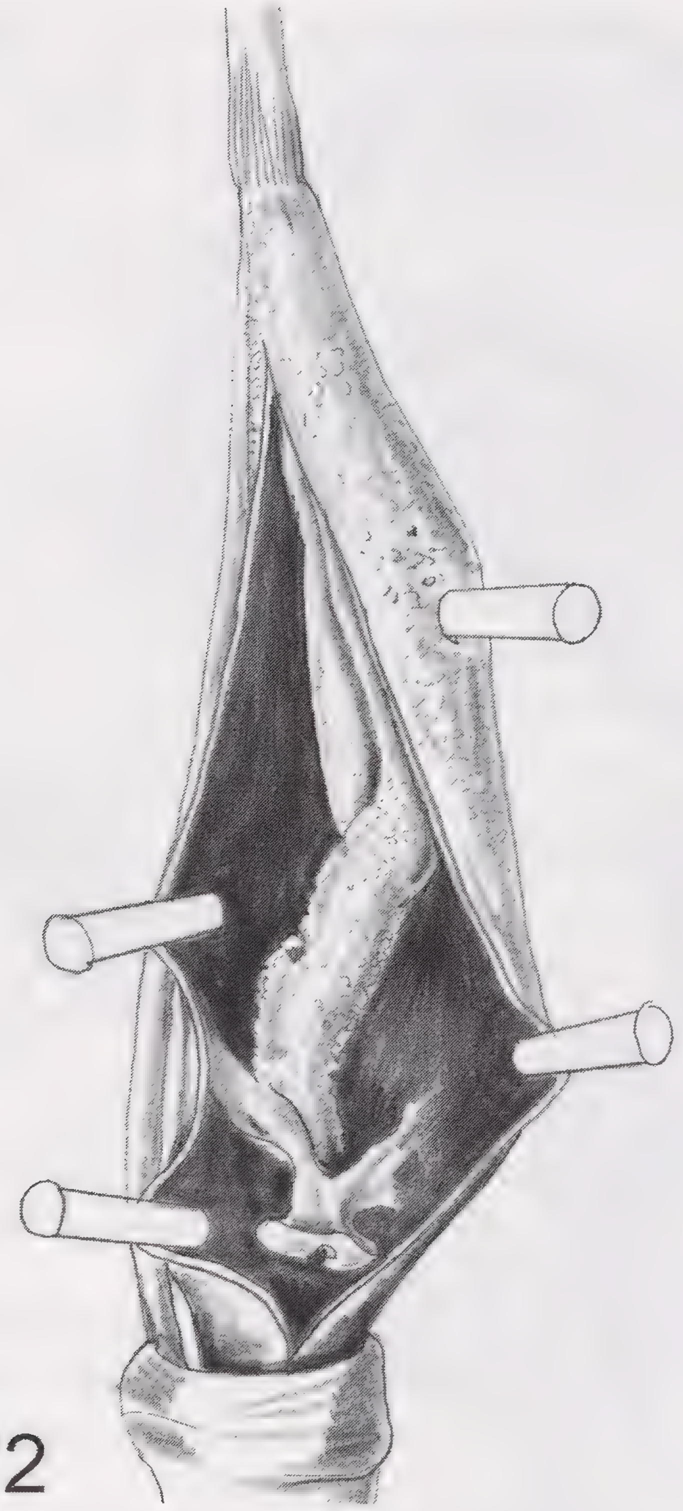
Hessemilimax kotulae (Westerlund, 1883) – Italy: Val di Tesero, Alpe di Pampeago, Rifugio Pampeago (Tesero, Trento), M. Bodon leg. 25.9.1994 (2 spirit specimens, FGC).

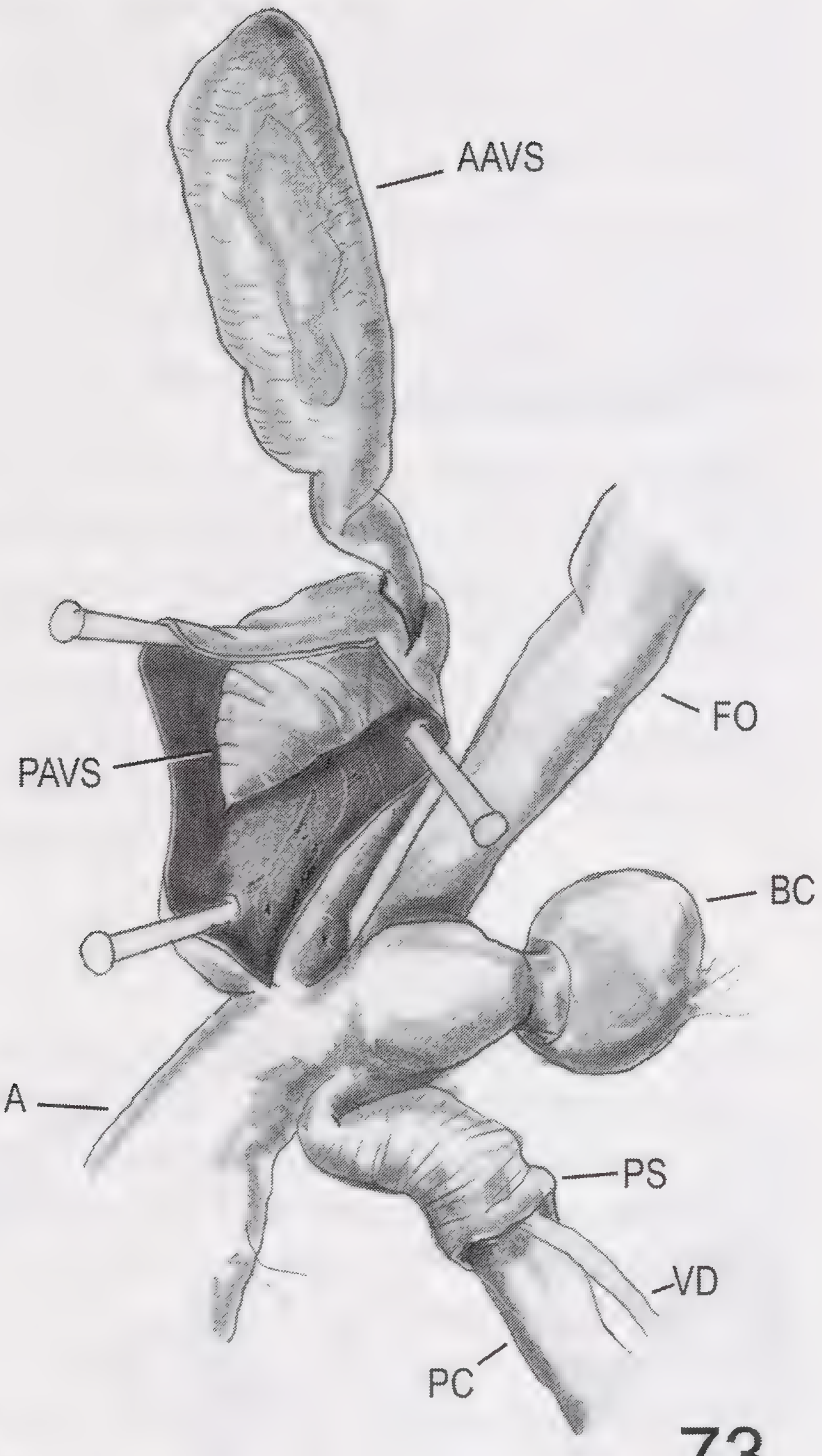


FIGS. 70, 71. Genitalia of a specimen of *Hessemilimax kotulae* (Westerlund, 1883) from Val di Tesero, Alpe di Pampeago, Rifugio Pampeago (Venetum, Italy), M. Bodon leg. 25.9.1994.

Diagnosis

Semislug-like vitrinids characterized by long penial retractor muscle arising from diaphragm, running in front of right optic nerve, below right ommatophore retractor and ending on penial complex subapically; stimulator atrial-vaginal, consisting of blind sac with apical portion covered by spongy glandular tissue and more or less invaginated into basal and internal





FIGS. 72, 73. *Hessemilimax kotulae* (Westerlund, 1883) from Val di Tesero, Alpe di Pampeago, Rifugio Pampeago (Venetum, Italy), M. Bodon leg. 25.9.1994. FIG. 72: Internal structure of penial complex; FIG. 73: Atrial-vaginal stimulator.

structures comprising only papilla of stimulator; penial complex with penial gland and penial sheath; vas deferens contacting penial complex distally, traversing penial sheath, running along penial complex and entering it subapically; internal structures of penial complex comprising two distinctive pilasters, possibly homologous with main and accessory pilasters; main pilaster consisting of slender, not distally lamellate, proximal glandular roll and very short distal muscular pleat ending in sort of π - shaped papilla.

Description of Type Species

Shell: vitriniform very dilated, glossy, thin and fragile, depressed, with approximately 1.8 whorls; last whorl extremely expanded; aperture very wide with columellar and basal margins bordered by broad periostracal fringe; columellar margin cut-away; umbilical area widely open; protoconch not prominent, smooth, with many regular spiral rows of very small pits; teleoconch smooth (Kerney & Cameron, 1979: pl. 6, fig. 4a, 4b).

Body: cannot be withdrawn completely into shell; right shell lobe large, covering wide portion of shell when animal undisturbed.

Radula: dichoglossan; marginal teeth unicuspid (Soós, 1917: 102, fig. 78).

Female Distal Genitalia (Figs. 70, 71, 73): free oviduct short and wide. Bursa copulatrix medium in size and sac-like, with short, slender duct, initially sligthly flared. Vagina very short, without glandula amatoria or other internal structures and without external glandular covering.

Male Distal Genitalia (Figs. 70–73): penial complex large and finger-like, with penial gland

and penial sheath. Penial gland covering most of proximal penial complex. Penial sheath long, curled up, arising from end of penial complex and enveloping almost all distal penial complex. Penial retractor arising from diaphragm, long, inserted apically. Vas deferens long, contacting penial complex distally, then traversing penial sheath, running along surface of penial gland and entering penial complex subapically near insertion of penial retractor. Internal structures of penial complex comprising two distinctive pilasters, possibly homologous with main and accessory pilasters. Main pilaster consisting of slender proximal glandular roll, not distally lamellate, and very short distal muscular pleat ending in sort of π-shaped papilla. Smaller pilaster (branch of main pilaster or accessory pilaster?) glandular, arising side by side with larger pilaster and ending about half its length. Vas deferens opening not visible, probably level with initial part of larger pilaster. Internal surface smooth.

Genital Atrium (Figs. 70, 71, 73): long and cylindrical, with sparse glandular covering and one side connected to body wall by thin muscular bands. Internal surface with sparse spongy tissue.

Atrial-Vaginal Stimulator (Figs. 70, 71, 73): very large and long, inserted between vagina and genital atrium, opposite to side entered by penial complex, and consisting of basal and apical portions, with apical more or less invaginated into basal. Basal portion sac-like, without external glandular covering. Apical portion with slender invaginated part, without external glandular covering and free part sac-like with spongy external glandular covering. Transverse sections of apical portion reveal absence of internal glandular layer equivalent to that present in glandula amatoria. Internal structures consisting of papilla of stimulator (conical structure absent). Papilla of stimulator short to long, conical, pointed, open at tip, protruding into basal portion. Internal surface of basal portion smooth.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: similar in juveniles and adults. Penial retractor long, passing below right ommatophore and in front of right optic nerve; distal genitalia lying right of right ommatophore retractor which consequently appears free of penial complex and vagina.

Mating: no data available.

Remarks

The monotypic *Hessemilimax* was introduced by Schileyko (1986) and apparently not regarded as valid by Hausdorf (2002).

Species of *Hessemilimax* and *Semilimax* share an atrial-vaginal stimulator composed of basal and apical portions, the apical being more or less invaginated into the basal portion which contains a rather large, long papilla. The stimulator is similar in general organization to the vaginal glandula amatoria but differs due to absence of an internal glandular layer.

Hessemilimax includes only one species (*H. kotulae*) and is distinguished from *Semilimax* by a long finger-like penial complex, a distinctive final part of main pilaster and absence of chitinous horn-like structure inside papilla of atrial-vaginal stimulator.

Some analyses indicated that *Hessemilimax* constitutes a monophyletic group with the species of *Semilimax* (Table 3). However, the basal relationships of this clade remained unresolved, like those between *Hessemilimax* and species of *Semilimax*.

Semilimacella Soós, 1917

Type Species: *Vitrina (Semilimacella) velebitica* Soós, 1917, by monotypy. *Vitrina velebitica* Soós is a junior synonym of *Vitrina reitteri* Boettger, 1880, according to Forcart (1960) and Schileyko (2003). In turn, *Vitrina reitteri* is a subspecies of *Semilimacella bonelli* (Targioni Tozzetti, 1873) according to Forcart (1960) and Schileyko (2003).

Synonyms

Balcanovitrina Osanova & Pintér, 1968. Type Species: *Balcanovitrina dojtshini* Osanova & Pintér, 1968, by monotypy.

Targionia Hesse, 1923 (*non* Signoret, 1869; Hemiptera). Type Species: *Vitrina bonelli* Targioni Tozzetti, 1873.

Tozzettia Hesse, 1924. New name for *Targionia* Hesse, 1923.

Material Examined

Semilimacella bonelli (Targioni Tozzetti, 1873) – Italy: Monti Reatini, Vallonina (Rieti), 33TUH30, F. Giusti leg. 20.11.1969 (2 spirit specimens, FGC); Monti Sibillini, Val Canatra (Norcia, Perugia), 33TUH54, F. Giusti & G. Manganelli leg. 13.9.1988 (1 spirit specimen, FGC).

Semilimacella cephalonica (Rähle, 1980) – Greece: Cefalonia Island, Ainos, W. Rähle leg. 24.9.1978 (4 spirit specimens, SMF 252354).

Diagnosis

Semislug-like vitrinids characterized by long penial retractor muscle arising from diaphragm, passing above right ommatophore retractor and ending on penial complex apically; stimulator atrial or vaginal, consisting of blind sac with apical portion covered by spongy glandular tissue and internal structures comprising one or two conical chitinous (at least in *S. bonelli*) structures; penial complex with penial gland and penial sheath; vas deferens contacting penial complex distally, traversing penial sheath, running along penial complex and entering it apically or proximally; internal structures of penial complex comprising only main pilaster consisting of large glandular roll divided into small, not distally lamellate, proximal portion and large medial-distal portion (at least in *S. bonelli*).

Description of Type Species

Shell: vitriniform slightly dilated, glossy, thin and fragile, depressed, with approximately 3.0 whorls; last whorl well expanded; aperture wide with basal margin bordered by narrow periostracal fringe; columellar margin normal; umbilicus closed; protoconch not prominent, smooth, with many regular spiral rows of very small pits; teleoconch smooth (Giusti et al., 1985: pl. 10, fig. H).

Body: cannot be withdrawn completely into shell; right shell lobe large, covering wide portion of shell when animal undisturbed.

Radula: dichoglossan; marginal teeth pluricuspid (Targioni Tozzetti, 1873: 20, pl. 6, fig. 3; Giusti, 1973: 465, pl. 4, figs. 1–3).

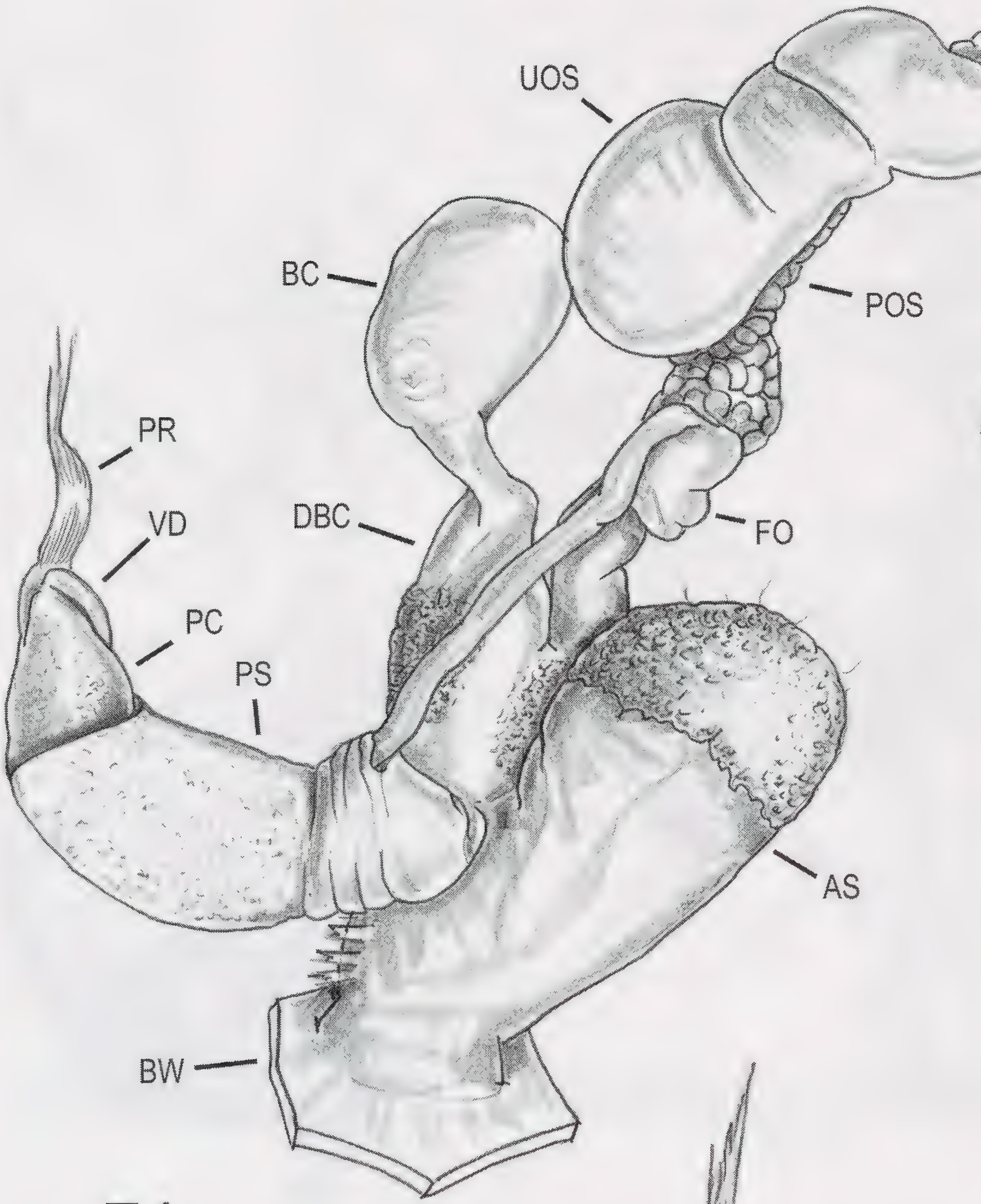
Female Distal Genitalia (Figs. 74, 75): free oviduct short and wide. Bursa copulatrix medium in size and sac-like, with short to medium, more or less slender duct, initially very flared. Vagina short, without glandula amatoria or other internal structures, but with external glandular covering on one side and initial part of duct of bursa copulatrix.

Male Distal Genitalia (Figs. 74, 75): penial complex large and club-like, with penial gland and penial sheath. Penial gland covering most of penial complex. Penial sheath long, arising from end of penial complex and enveloping almost all penial complex. Penial retractor arising from diaphragm, long, inserted apically. Vas deferens long, contacting penial complex distally, then traversing penial sheath, running along surface of penial gland and entering penial complex apically near insertion of penial retractor. Internal structures of penial complex comprising main pilaster only which consists of large glandular roll divided into small whitish proximal portion, slightly lobate, not distally lamellate, and large but progressively more slender medial–distal portion, ending before genital atrium. Vas deferens opening in small slit, level with proximal penial complex. Internal surface with thin parallel segmented mainly transverse pleats.

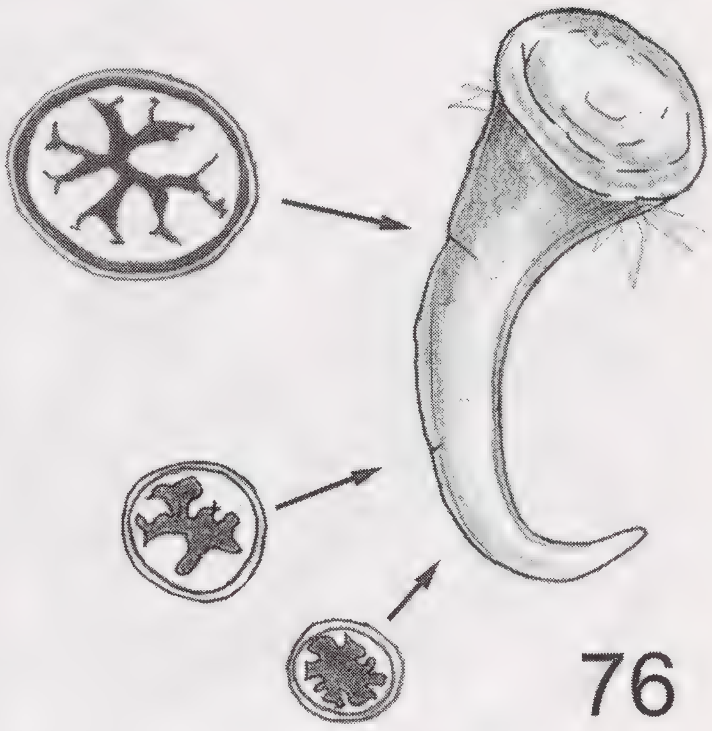
Genital Atrium (Figs. 74, 75): short, with large club-like atrial stimulator and one side connected to body wall by thin muscular bands. Internal structures consisting of proximal semicircular crest forming sort of bulkhead level with tips of horn-like structures of atrial stimulator and close to opening of duct of bursa copulatrix. Internal surface smooth.

Atrial Simulator (Figs. 74–76): large and club-like, entering genital atrium opposite to side entered by penial complex, and consisting of basal and apical portions. Basal portion tubular, without external glandular covering. Apical portion cap-like, with thick spongy external glandular covering and internal compact mass of tissue. Internal structures comprising two conical structures ("brachia copulatoria"; Schileyko, 2003), similar in shape but different in size, with rather resistant yellowish subtransparent chitinous walls and internal cavity partly filled with whitish material; conical structures with bases lodged into compact mass of tissue filling apical portion (but not firmly connected to it being rather easily removed) and pointed tips reaching genital atrium. Internal surface of basal portion smooth.

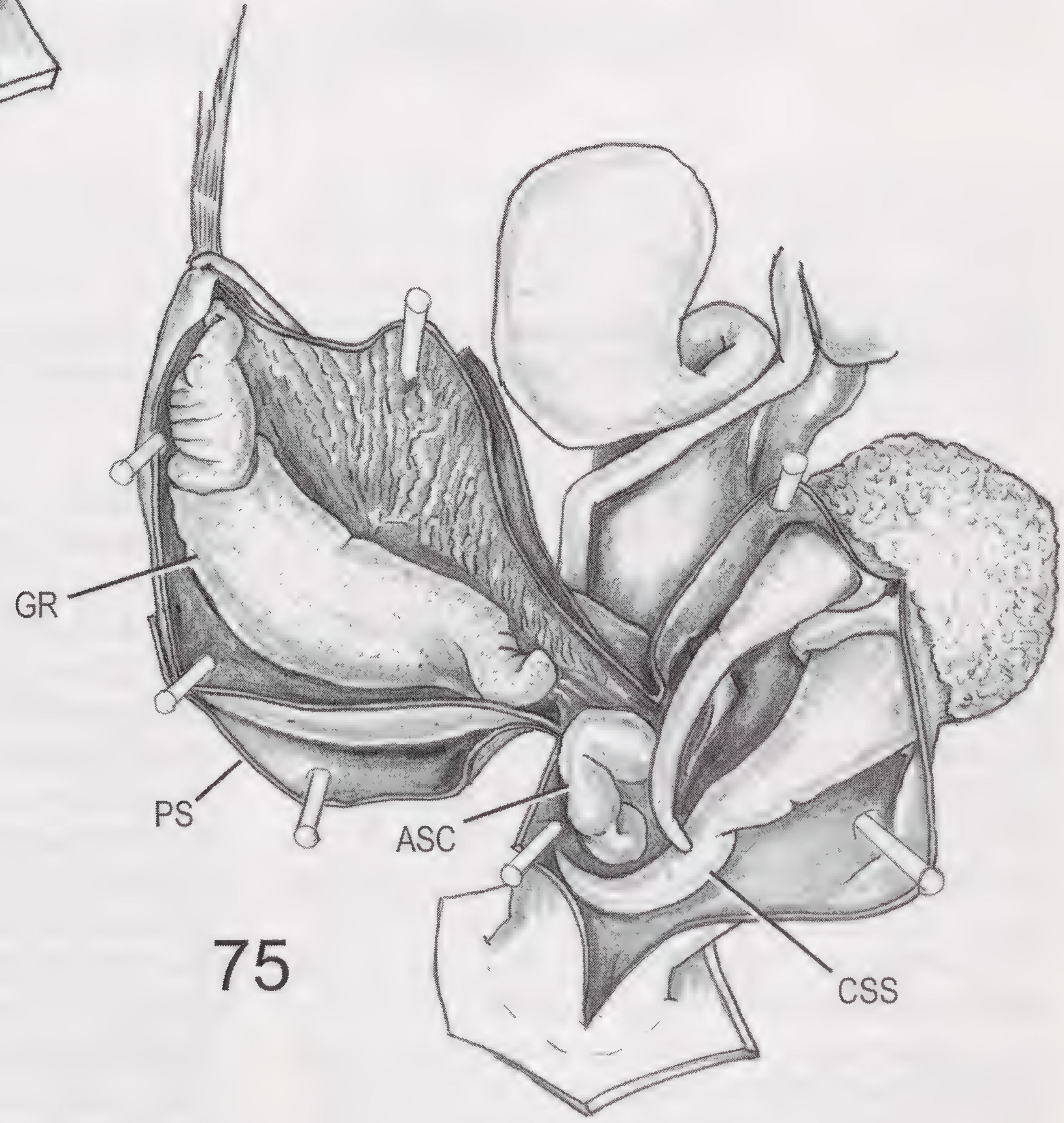
Relationships Between Right Ommatophore Retractor and Distal Genitalia: similar in juveniles and adults (Fig. 11). Penial retractor long, passing above right ommatophore retractor which is consequently free of penial complex and vagina (right ommatophore retractor is below penial complex and above atrial stimulator).



74



76



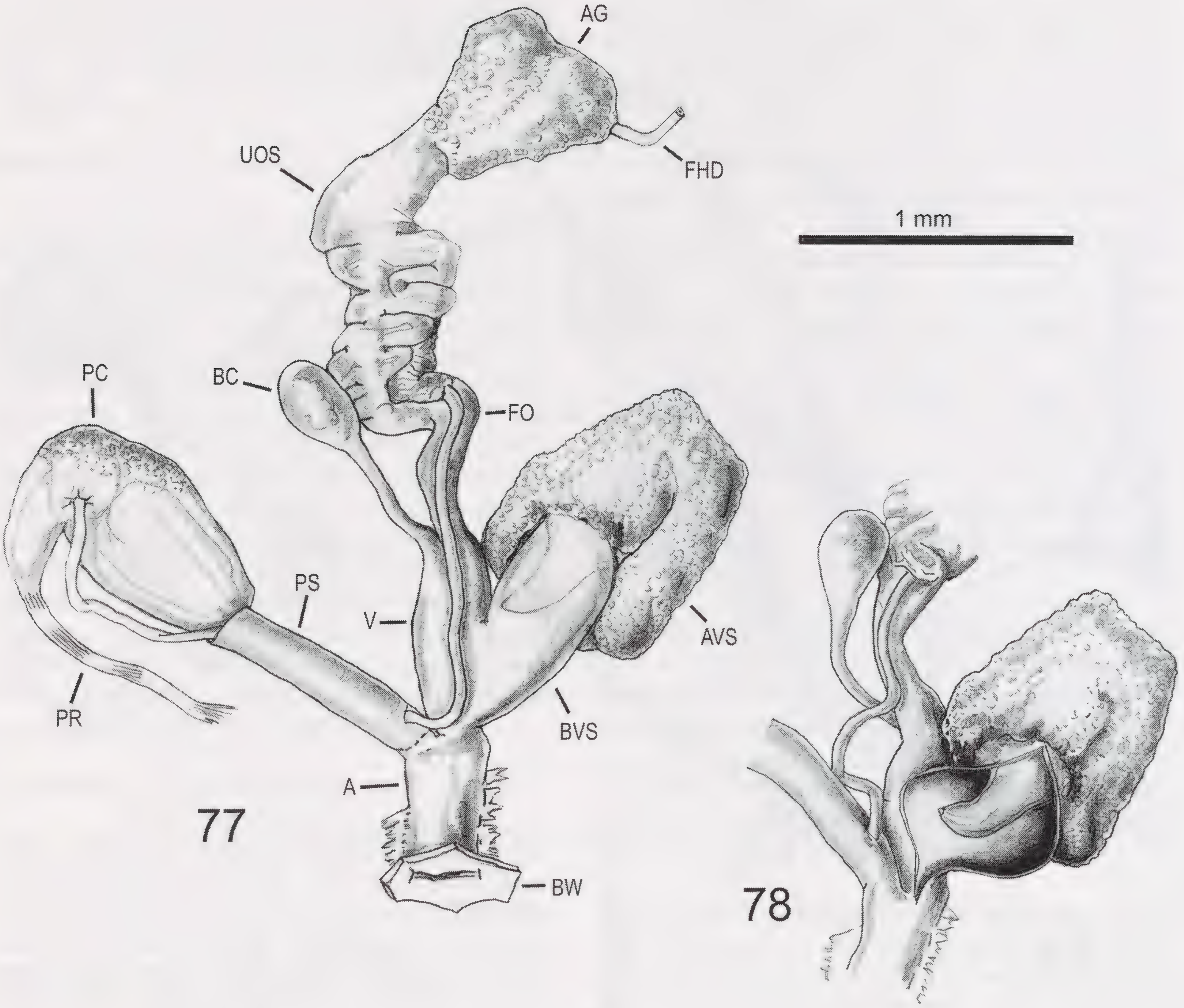
75

74 - 76 2 mm

1 mm

sections of Fig. 76

FIGS. 74–76. *Semilimacella bonelli* (Targioni Tozzetti, 1873) from Monti Reatini, Vallonina (Latium, Italy), F. Giusti leg. 20.11.1969. FIG. 74: Distal genitalia; FIG. 75: Internal structure of penial compex and vagina; FIG. 76: An isolated conical structure.



FIGS. 77, 78. FIG. 77: Distal genitalia; FIG. 78: Internal stucture of vaginal stimulator. *Semilimacella cephalonica* (Rähle, 1980) from Cefalonia Island, Ainos (Greece), W. Rähle leg. 24.9.1978.

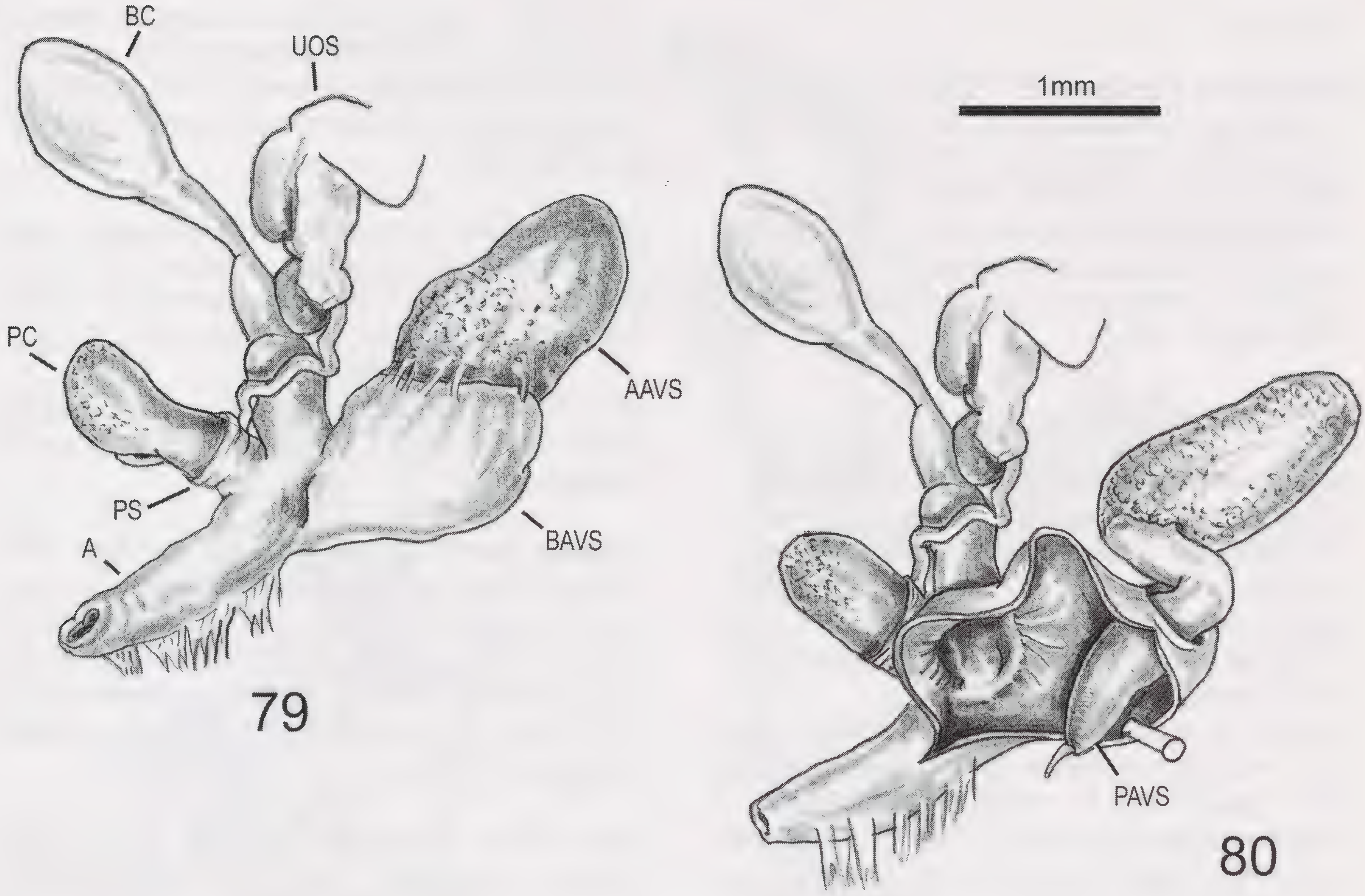
Mating: no data available.

Remarks

Semilimacella was introduced by Soós (1917) as a subgenus of *Vitrina*. It has since been regarded as a junior synonym of *Semilimax* (Baker, 1929; Thiele, 1931), a subgenus of *Vitrina* (Zilch, 1959), a junior synonym of *Oligolimax* (Forcart, 1965) and finally a distinct genus (Damjanov & Likharev, 1975).

According to Hausdorf (2002), *Semilimacella* includes only three species from the Alps, Apennines, Balkans and central Europe (major anatomical references on which are: Targioni Tozzetti, 1873; Forcart, 1960; Rähle, 1980; Mildner, 1982) and is the sister group of *Vitrina*; in turn *Semilimacella* + *Vitrina* are the sister group of (*Eucobresia* (*Phenacolimax* ((*Plutonia*, *Oligolimax*) (*Arabivitrina*, *Calidivitrina*)))).

The atrial stimulator of *Semilimacella* is completely different from that of *Semilimax* and *Hessemilimax*, the only other vitrinids with an atrial or atrial-vaginal stimulator: it is shorter and its apical part is not invaginated into the basal portion. Its apical part is somewhat bilobate with a thick external layer of glandular tissue and is not hollow internally. Tissue filling the apical part is compact, muscular in appearance and lodges the base of two conical structures which have rather long, tapered pointed tips extending into the lumen and as far as the genital atrium. These two structures have cuticularized, thin but resistant chitinous-like walls and contain whitish condensed material adhering to internal



FIGS. 79, 80. *Semilimax semilimax* (Férussac, 1802) from Plitvička Jesera (Croatia), A. Minelli leg. 13.4.1968. FIG. 79: Distal genitalia; FIG. 80: Internal structure of distal genitalia.

wall surfaces; these horn-like structures are easily detached from their muscular support and their base is closed, so that there is no evidence of direct communication between their lumen and the glandular mass inside "cul de sac" of stimulator. Nature and origin of whitish material is unknown.

Two other species, *S. carniolica* (Boettger, 1884) and *S. cephalonica*, are assigned to *Semilimacella* by Hausdorf (2002), but many details of their anatomy are unclear. Remarkably, their stimulator is sometimes reported as distally bilobate and vaginal (Rähle, 1980; Mildner, 1982; Schileyko, 2003). We tried to re-examine them but unfortunately our attempt to find spirit specimens of *S. carniolica* were unsuccessful. Re-examination of *S. cephalonica* (Figs. 77, 78) confirmed most details reported by Rähle (1980) and showed that this species and *S. bonelli* share some characters (penial sheath; penial retractor passing above right ommatophore retractor; club-like stimulator with apical glandular cap), but differ in many others (duct of bursa copulatrix initially very flared in *S. bonelli*, not flared in *S. cephalonica*; vas deferens entering penial complex apically in *S. bonelli*, proximally in *S. cephalonica*; stimulator atrial with a small, cap-like, spongy external glandular covering and two internal conical chitinous structures in *S. bonelli*, vaginal with large cap-like spongy external glandular covering and only one internal conical structure in *S. cephalonica*).

Only BI recovered the two *Semilimacella* species as a monophyletic group whereas AP suggested that they could be a paraphyletic group (*S. cephalonica* (*S. bonelli*, *V. pellucida*)) belonging to a larger monophyletic group, including three other species (*Oligolimax annularis*, *O. musignani* and *Sardovitrina polloneriana*) on the basis of the exclusive disposition of the penial retractor above the right ommatophore retractor.

Semilimax Stabile, 1859

Type Species: *Vitrina elongata* Draparnaud, 1805, by subsequent designation (Fischer in: Paulucci, 1878) (*V. elongata* is a junior synonym of *Helix semilimax* Férussac, 1802).

Synonyms

Chlamydea Westerlund, 1886. Type Species: *Vitrina bicolor* Westerlund, 1886, by monotypy (according to Bank et al., 2001).

Vitrinopugio von Ihering, 1892. Type Species: *Vitrina elongata* Draparnaud, 1805, by subsequent designation (Hesse, 1923) (*V. elongata* is a junior synonym of *Helix semilimax* Férussac, 1802).

Material Examined

Semilimax carinthiacus (Westerlund, 1886) – Italy: Laghi di Fusine (Tarvisio, Udine), A. Minelli leg. 22.8.1972 (1 spirit specimen, FGC).

Semilimax pyrenaicus (Férussac, 1821) – France: Lac d'Oredon, G. Marcuzzi leg. (2 spirit specimens, FGC).

Semilimax semilimax (Férussac, 1802) – Austria: Hochkönig, Dienten, Sessellift-Bergstation (Salzburg), O. Paget leg. 30.7.1973 (2 spirit specimens, NHMW 74239); Saalbach, bei Haus Hapimag (Salzburg), O. Paget leg. 4.7.1972 (2 spirit specimens, NHMW 77954). Croatia: Plitvička Jesera, A. Minelli leg. 13.4.1968 (1 spirit specimen, FGC).

Diagnosis

Semislug-like vitrinids characterized by absence of penial retractor (but in one species long, arising from diaphragm, running in front of right optic nerve, below right ommatophore retractor and ending on penial complex subapically); stimulator atrial-vaginal, consisting of blind sac with apical portion covered by spongy glandular tissue and more or less invaginated into basal and internal structures comprising only papilla of stimulator traversed by chitinous hook-like structure (absent in one species); penial complex with penial gland and penial sheath; vas deferens contacting penial complex distally, traversing penial sheath, running along penial complex and entering it subapically; internal structures of penial complex comprising only main pilaster, consisting of large, not distally lamellate, proximal glandular roll.

Description of Type Species

Shell: vitriniform very dilated, glossy, thin and fragile, depressed, with approximately 1.8 whorls; last whorl extremely expanded; aperture very wide with columellar and basal margins bordered by broad periostracal fringe; columellar margin slightly cut-away; umbilical area open; protoconch not prominent, smooth, with many regular spiral rows of very small pits; teleoconch smooth (Kerney & Cameron, 1979: pl. 6, fig. 3a–c).

Body: cannot be withdrawn completely into shell; right shell lobe large, covering wide portion of shell when animal undisturbed (Falkner, 1990: fig. 2 at p. 173; 1992: fig. 2 at p. 270).

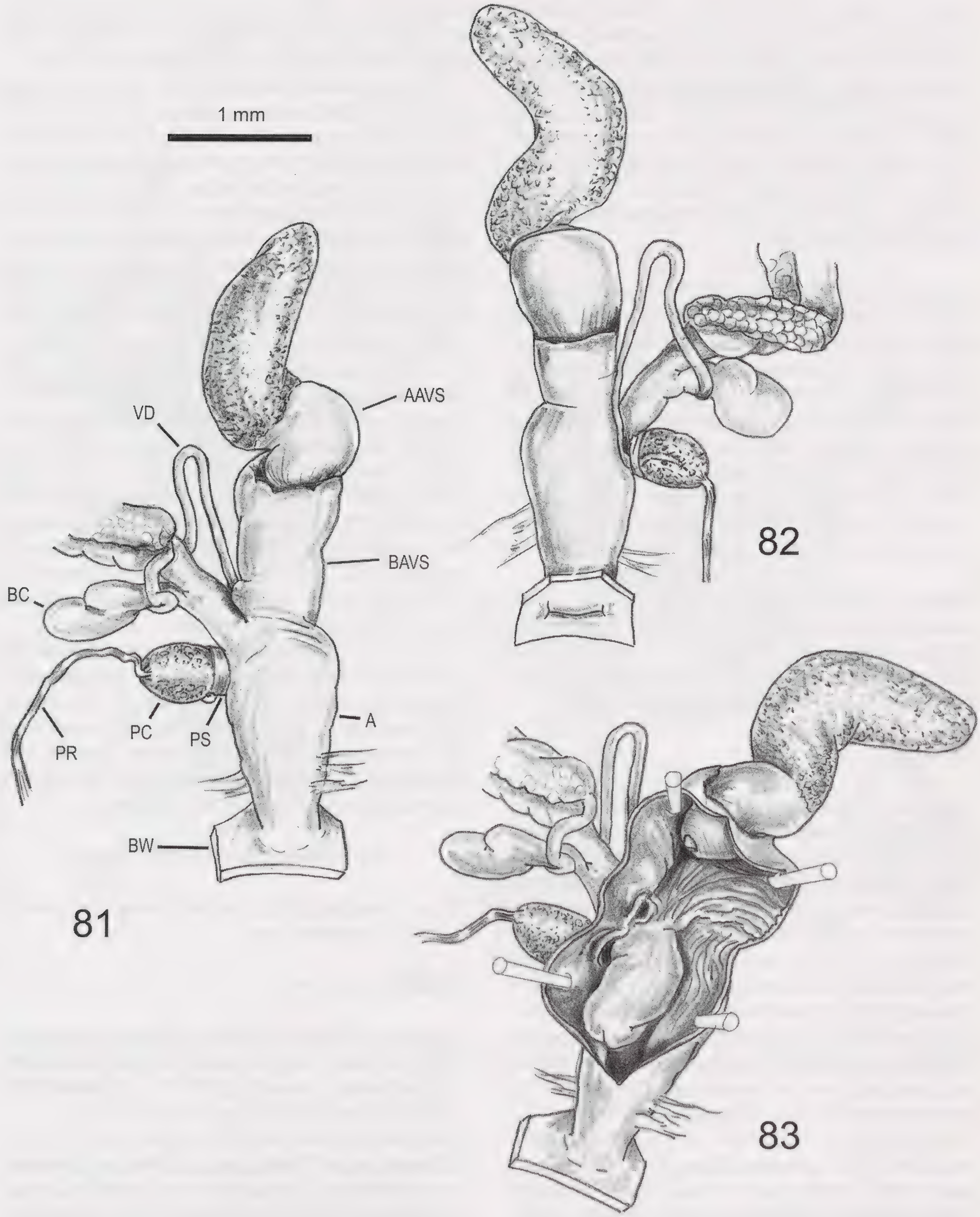
Radula: dichoglossan; marginal teeth unicuspid (Wagner, 1915: 474, pl. 11, fig. 83 a, b, as *S. elongatus*).

Female Distal Genitalia (Figs. 79, 80): free oviduct short and wide. Bursa copulatrix medium in size and sac-like, with short to medium, more or less slender duct, initially not flared. Vagina short, without glandula amatoria or other internal structures and without external glandular covering.

Male Distal Genitalia (Figs. 79, 80): penial complex very small and club-like, with penial gland and penial sheath. Penial gland covering most of proximal penial complex. Penial sheath short, arising from end of penial complex. Penial retractor absent (other *Semilimax* species have penial retractor arising from diaphragm, long, inserted apically). Vas deferens long, contacting penial complex distally, then traversing penial sheath, running along surface of penial gland and entering penial complex subapically. Internal structures of penial complex comprising main pilaster only which consists of large glandular roll, not distally lamellate, ending before genital atrium. Vas deferens opening not visible, probably level with initial part of glandular roll. Internal surface smooth.

Genital Atrium (Figs. 79, 80): long and cylindrical, with one side connected to body wall by thin muscular bands. Internal surface smooth.

Atrial-Vaginal Stimulator (Figs. 79, 80): very large and long, inserted between vagina and genital atrium, opposite to side entered by penial complex, and consisting of basal and apical portions, with apical more or less invaginated into basal portion. Basal portion sac-like or cylindrical, without external glandular covering. Limit between apical and basal portions marked by transverse groove, originating by invagination of apical into basal portion. Apical portion with invaginated part slender, without external glandular covering, and free part



FIGS. 81–83. *Semilimax carinthiacus* (Westerlund, 1886) from Laghi di Fusine (Friuli-Venetia Giulia, Italy), A. Minelli leg. 22.8.1972. FIGS. 81, 82: Distal genitalia; FIG. 83: Internal structure of distal genitalia.

sac-like, with thick spongy external glandular covering. Transverse sections of apical portion reveal absence of internal glandular layer equivalent to that in glandula amatoria. Internal structures consisting only of papilla of stimulator traversed by hook-like structure. Papilla of stimulator pointed, open at tip, protruding into basal portion. Hook-like structure ("Conchinspitze", Künkel, 1933; "thorn of sarcobelum", Schileyko, 2003), somewhat recalling those of *Semilimacella*, with very thin apparently chitinous walls, present inside invaginated part of apical portion; it has wide base and very slender pointed tip which usually protrudes out of stimulator papilla (Fig. 2; see also Wagner, 1915: fig. 141; Künkel, 1933: figs. 7C, 9A, 12; Schileyko, 2003: fig. 1914). Internal surface of basal portion smooth.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: due to the fact that penial retractor is absent, right ommatophore retractor is free of distal genitalia. In other *Semilimax* species (e.g., *S. carinthiacus*, Fig. 4) they are similar in juveniles and adults: penial retractor long and slender, passing below right ommatophore and in front of right optic nerve; distal genitalia lying right of right ommatophore retractor which consequently appears free of penial complex and vagina.

Mating: described by Künkel (1933). After protruding out of papilla of stimulator, hook-like structure produces sucker-like structure that attaches to partner's body; everted penis inserts into vagina, transferring spermatic mass.

Remarks

Semilimax was established by Stabile (1859) with seven species originally included. Overlooking Fischer's designation (in: Paulucci, 1878) of *Vitrina elongata* Draparnaud, 1805, as the type species, Hesse (1923) considered *Semilimax* a subgenus of *Phenacolimax*, corresponding to the group of *Vitrina diaphana* (i.e., to the species now included in *Eubobresia*). Few years later, Baker (1929) corrected Hesse's misinterpretation, restoring the correct sense of this taxon. *Semilimax* was thus considered a distinct genus by all subsequent authors except Thiele (1931), who regarded it as a subgenus of *Vitrina*.

According to Hausdorf (2002), *Semilimax* includes five species from Europe (major anatomical references on which are: Boycott, 1914; Hesse, 1923; Soós, 1924; Künkel, 1933; Forcart, 1956; Schileyko, 1986; Hausdorf, 2002) and has unresolved relationships with *Vitrinobrachium* and ((*Semilimacella*, *Vitrina*) (*Eucobresia* (*Phenacolimax* ((*Plutonia*, *Oligolimax*) (*Arabivitrina*, *Calidivitrina*))))).

Species of *Hessemilimax* and *Semilimax* share an atrial-vaginal stimulator composed of apical sac-like glandular part and basal part, containing a rather large, long papilla. The stimulator is similar in general organization to the vaginal glandula amatoria but different due to the absence of an internal glandular layer.

Two species of *Semilimax* (*S. semilimax* and *S. carinthiacus*) have a hook-like structure (reminiscent of the conical structures of the stimulator of *Semilimacella*?) inside the invaginated portion of the apical part of the atrial-vaginal stimulator. The hook-like structure has very thin, apparently cuticularized walls, a rather large basal portion and a very slender pointed tip, lodged inside the lumen of the papilla. The tip usually protrudes from the apical opening. Davison & Mordan (2005) claimed that it is homologous to a dart.

S. pyrenaicus and *S. semilimax* lack the penial retractor (they differ for the shell shape: ear-like, with columellar margin of peristome slightly cut-away in the first; typical vitriniform, with columellar margin of peristome normal in the second). *Semilimax carinthiacus* has penial retractor and a large outgrowth inside the genital atrium, situated between openings of penis and vagina (Figs. 81–83), and is characterized by shell with rather normal columellar margin of peristome (i.e., not cut-away).

Some analyses found that species of *Semilimax* constitute a differently supported, monophyletic group with *Hessemilimax* (Table 3). The basal relationships of this clade remained unresolved like those between its members, though MP recovered a subclade consisting of *Semilimax pyrenaicus* and *S. semilimax* (Table 3).

Vitrinobrachium Künkel, 1929

Type Species: *Helicolimax breve* Férussac, 1821, by monotypy.

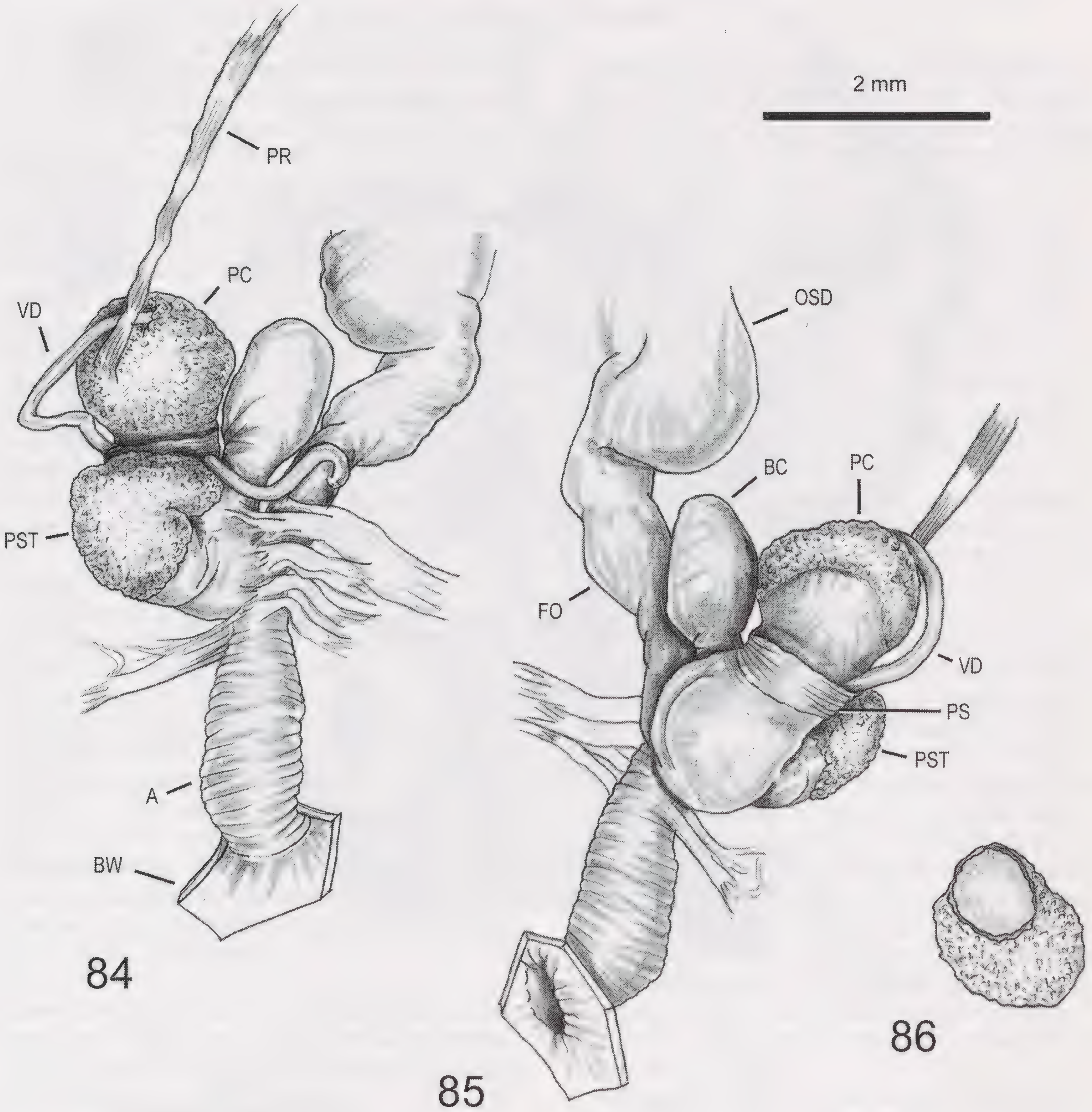
Material Examined

Vitrinobrachium baccetti Giusti & Mazzini, 1971 – Italy: Alpi Apuane, Monte Freddone (Stazzema, Lucca), 32TPP07, F. Giusti leg. 29.9.1969 (7 spirit specimens, FGC).

Vitrinobrachium breve (Férussac, 1821) – Italy: Altopiano del Cansiglio, La Crosetta (Treviso), 33TTM9901, F. Giusti leg. 11.11.1976 (2 spirit specimens, FGC). Altopiano del Cansiglio, Monte Pizzoc (Treviso), 33TTM9901, F. Giusti leg. 11.11.1976 (2 spirit specimens, FGC).

Diagnosis

Semislug-like vitrinids characterized by long penial retractor muscle arising from columellar muscle, running in front of right optic nerve, below right ommatophore retractor and ending



FIGS. 84–86. *Vitrinobrachium breve* (Férussac, 1821) from Altopiano del Cansiglio, La Crosetta (Venetum, Italy), F. Giusti leg. 11.11.1976. FIGS. 84, 85: Distal genitalia; FIG. 86: Transverse section of stimulator.

on penial complex subapically; stimulator penial, consisting of blind sac with apical portion covered by spongy glandular tissue and internal structures comprising only pedunculate sucker; penial complex with penial gland and penial sheath; vas deferens contacting penial complex medially, traversing penial sheath, running along penial complex and entering it subapically; internal structures of penial complex very distinctive, comprising sort of flat glans, divided into two semicircular tiles, and wrinkled crest.

Description of Type Species

Shell: vitriniform very dilated, glossy, thin and fragile, depressed, with approximately 1.8 whorls; last whorl extremely expanded; aperture very wide with columellar and basal margins bordered by broad periostracal fringe; columellar margin normal; umbilicus closed; protoconch not prominent, smooth, with many regular spiral rows of very small pits; teleoconch smooth (Kerney & Cameron, 1979: pl. 6, fig. 2a–c).

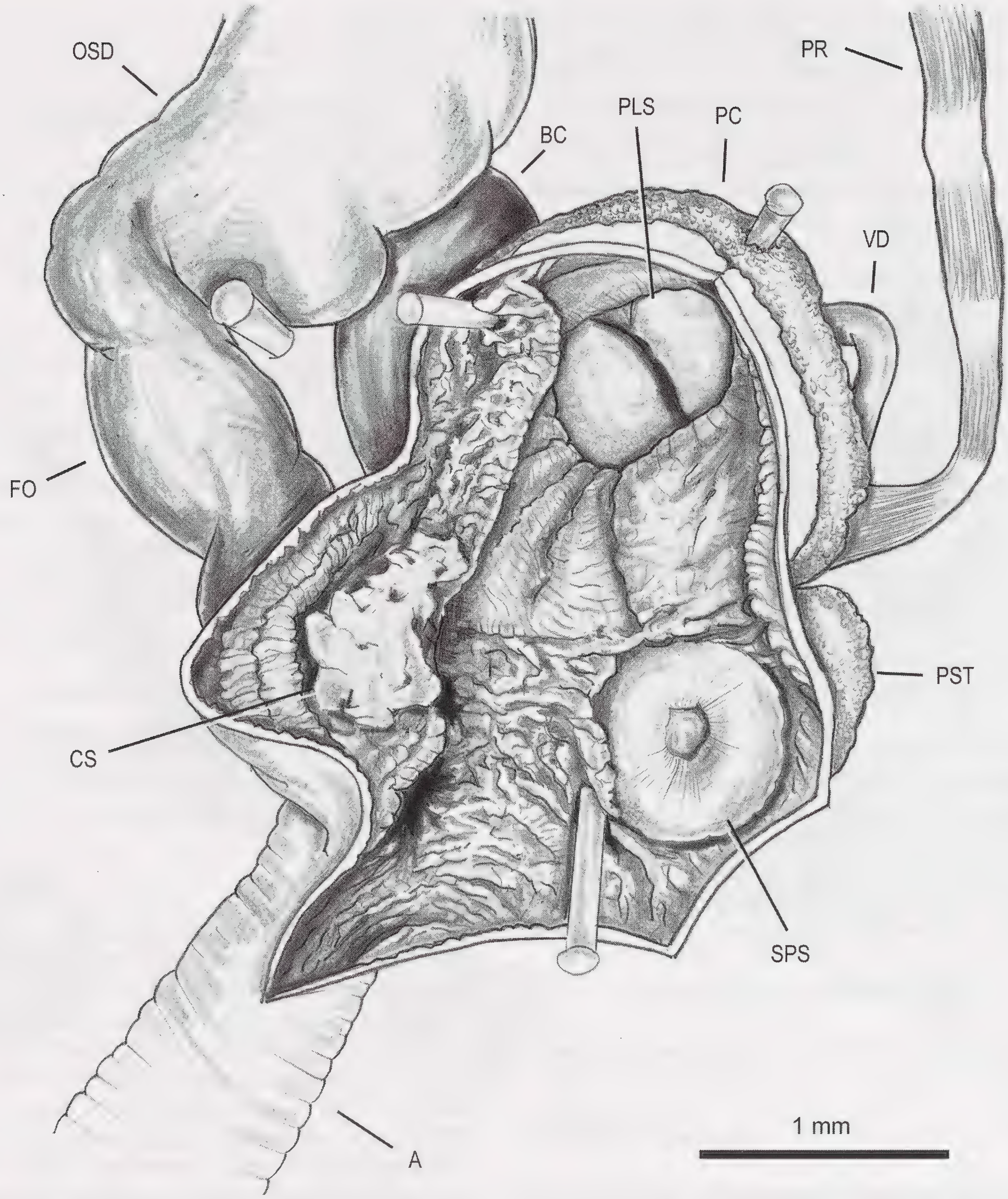


FIG. 87. Internal structure of distal genitalia of a specimen of *Vitrinobrachium breve* (Férussac, 1821) from Altopiano del Cansiglio, La Crosetta (Venetum, Italy), F. Giusti leg. 11.11.1976.

Body: cannot be withdrawn completely into shell; right shell lobe large, covering wide portion of shell when animal undisturbed (Kerney & Cameron, 1979: pl. 6, fig. 2d; Falkner, 1990: fig. 3 at p. 173; 1992: figs. 3–5 at p. 270).

Radula: dichoglossan; marginal teeth unicuspid (Wagner, 1915: 475, pl. 11, fig. 84).

Female Distal Genitalia (Figs. 84, 85, 87): free oviduct short and wide. Bursa copulatrix medium in size and oval, with short, slender to wide duct, initially not flared; bursa copulatrix duct entering distal penial complex (not proximal vagina) on side opposite to that with penial stimulator. Vagina absent.

Male Distal Genitalia (Figs. 84–87): penial complex large and globular, with penial gland, penial sheath and distally, on opposite sides, penial stimulator and bursa copulatrix. Penial gland covering most of penial complex. Penial sheath short, arising from mid penial complex. Penial retractor arising from columellar muscle, long, inserted subapically. Vas deferens long, contacting penial complex medially, then traversing penial sheath and entering penis subapically near insertion of penial retractor. Internal structures of penial complex very distinctive and therefore difficult to homologize, comprising sort of flat glans and wrinkled crest. Flat glans, divided into two semicircular tiles by rather wide groove, is located in correspondence with thick cap formed by penial gland. Wrinkled undulating crest arises close to glans and ends in proximal genital atrium. Vas deferens opening in wide groove dividing glans into two semicircular tiles. Internal surface with longitudinal, very segmented pleats, diffuse spongy tissue with crypts, and sometimes variably large masses of coagulated secretion.

Penial Stimulator (Figs. 84–87): rather large, club-like or globular, entering distal penial complex opposite to side entered by duct of bursa copulatrix and consisting of basal and apical portions. Basal portion tubular, without external glandular covering. Apical portion cap-like, with thick external glandular covering and internal compact mass of tissue. Internal structures consisting of pedunculate sucker-like structure hollow at centre, lodged into compact mass of tissue filling apical portion. Internal surface of basal portion with spongy tissue and, sometimes, variably large masses of coagulated secretion.

Genital Atrium (Figs. 84, 85, 87): long to very long and cylindrical, with one side connected to body wall by robust muscular bands. Internal surface as in penial complex.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: similar in juveniles and adults (Fig. 8). Penial retractor long, passing below right ommatophore and in front of right optic nerve; distal genitalia lying right of right ommatophore retractor which therefore appears free of penial complex and vagina.

Mating: described by Künkel (1929, 1933). Pedunculate sucker of stimulator attaches to partner's body and everted penial complex rolls up around everted stimulator; spermatic mass is attached to everted stimulator; then everted penial complex detaches from sucker peduncle and everted stimulator with spermatic mass is withdrawn inside body.

Remarks

Vitrinobrachium was introduced by Künkel (1929) as a distinct genus and has been regarded as such by all subsequent authors (Forcart, 1944; Zilch, 1959; Schileyko, 1986, 2003; Hausdorf, 2002).

According to Hausdorf (2002), *Vitrinobrachium* includes three species from western Europe (major anatomical references on which are: Wagner, 1915; Hesse, 1923; Künkel, 1933; Forcart, 1956; Giusti & Mazzini, 1971; Schileyko, 1986; Hausdorf, 2002; Nardi et al., 2007) and has unresolved relationships with *Semilimax* and ((*Semilimacella*, *Vitrina*) (*Eucobresia* (*Phenacolimax* ((*Plutonia*, *Oligolimax*) (*Arabivitrina*, *Calidivitrina*))))).

Apart from the type species, *Vitrinobrachium* includes only two species: *V. baccettii* from the Ligurian and Tuscan Apennines and Apuan Alps (Italy) and *V. tridentinum* Forcart, 1956, from Trentino - Alto Adige (Italy) (anatomy: Forcart, 1956; Nardi et al., 2007). Populations which differ considerably from typical specimens are assigned to these species, but they may be distinct taxa.

The species of *Vitrinobrachium* form a well-distinguished group, sharing many distinctive characters: penis with internal, glans-like structure, flat and divided into two parts; stimulator penial (erroneously considered atrial by Schileyko, 1986, and Hausdorf, 2002; vaginal by Muratov, 1999) in form of a club-like appendix (*V. breve* and *V. tridentinum*) or fused and englobed in distal part of penis (*V. baccettii*) with internal pedunculate sucker-like structure; vagina absent; duct of bursa copulatrix entering distal penis; penial retractor arising from columellar muscle.

All analyses found that *Vitrinobrachium* is monophyletic and supported by numerous synapomorphies (Figs. 14, 15; Table 3), although its deep relationships remain unresolved.

Vitrinids without Vaginal or Diverticular Stimulator

Vitrinids without vaginal or diverticular stimulator include three taxa of the genus group (*Calidivitrina*, *Eucobresia* and *Vitrina*), though other species with similar features belong to other genera, usually having the glandula amatoria (*Azorivitrina brevispira* and "*Madeirovitrina*" *media*). Our phylogenetic analyses suggested that they are derived taxa, which arose independently by loss of vaginal or diverticular stimulators.

Calidivitrina Pilsbry, 1919

Type Species: *Vitrina oleosa* Martens, 1895, by original designation.

Material Examined

Calidivitrina cf. *oleosa* (Martens, 1895) – Kenya: Cherangani near Kitale, 3000 m, A. Jeannel leg. 10.3.1933 (2 spirit specimens consisting of one already dissected adult and one intact juvenile, MNHN).

Diagnosis

Semislug-like vitrinids characterized by (short?) penial retractor muscle arising from diaphragm, compelling penial complex below right ommatophore and in front of right optic nerve and ending on penial complex subapically (at least in juveniles); stimulator absent; penial complex with penial gland and without penial sheath; vas deferens entering penial complex proximally; internal structures of penial complex comprising only main pilaster, consisting of large, distally lamellate, glandular roll and smooth slender distal muscular pleat.

Description of Type Species

Shell: vitriniform typical, glossy, thin and fragile, depressed, with approximately 3.0 whorls; last whorl expanded; aperture moderately wide; border of columellar and basal margins unknown; columellar margin normal; umbilicus closed; protoconch not prominent, smooth, without spiral rows of pits; teleoconch smooth (Pilsbry, 1919: 282, fig. 143a, b).

Body: available data uncertain (Martens, 1895; Pilsbry, 1919; Verdcourt, 2005). According to Pilsbry (1919: 283), shell lobes absent or, if present, very small. However Verdcourt (2005: 150, 152) stated that shell lobes are very well developed in most *Calidivitrina* species and sometimes cover whole shell.

Radula: dichoglossan; marginal teeth unicuspid (Pilsbry, 1919: 283; Hubendick, 1953: 89).

Female Distal Genitalia (Figs. 88–90): free oviduct short and wide. Bursa copulatrix medium in size and globular, with short, slender duct, initially not flared. Vagina short, without glandula amatoria, but with internal proximal pad. Internal surface of distal vagina with thin pleats, variably arranged.

Male Distal Genitalia (Figs. 88–90): penial complex large and club-like, with penial gland and without penial sheath. Penial gland covering most of proximal penial complex. Penial retractor arising from diaphragm, (short?), inserted apically. Vas deferens medium in length, entering penial complex proximally, thus distinguishing short pointed flagellum and penis proper. Internal structures of penial complex comprising main pilaster only which consists of large proximal glandular roll, distally lamellate, and slender smooth distal muscular pleat, ending in proximal genital atrium. Vas deferens opening not visible, probably level with glandular roll. Internal surface with thin irregularly arranged pleats or smooth.

Genital Atrium (Figs. 88–90): very long and cylindrical, with one side connected to body wall by thin muscular bands. Internal surface as in penial complex.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: unknown in adults but juveniles with entire penial complex below right ommatophore and in front of right optic nerve; right ommatophore is consequently shifted to right and compelled to lie between penial complex and vagina.

Mating: no data available.

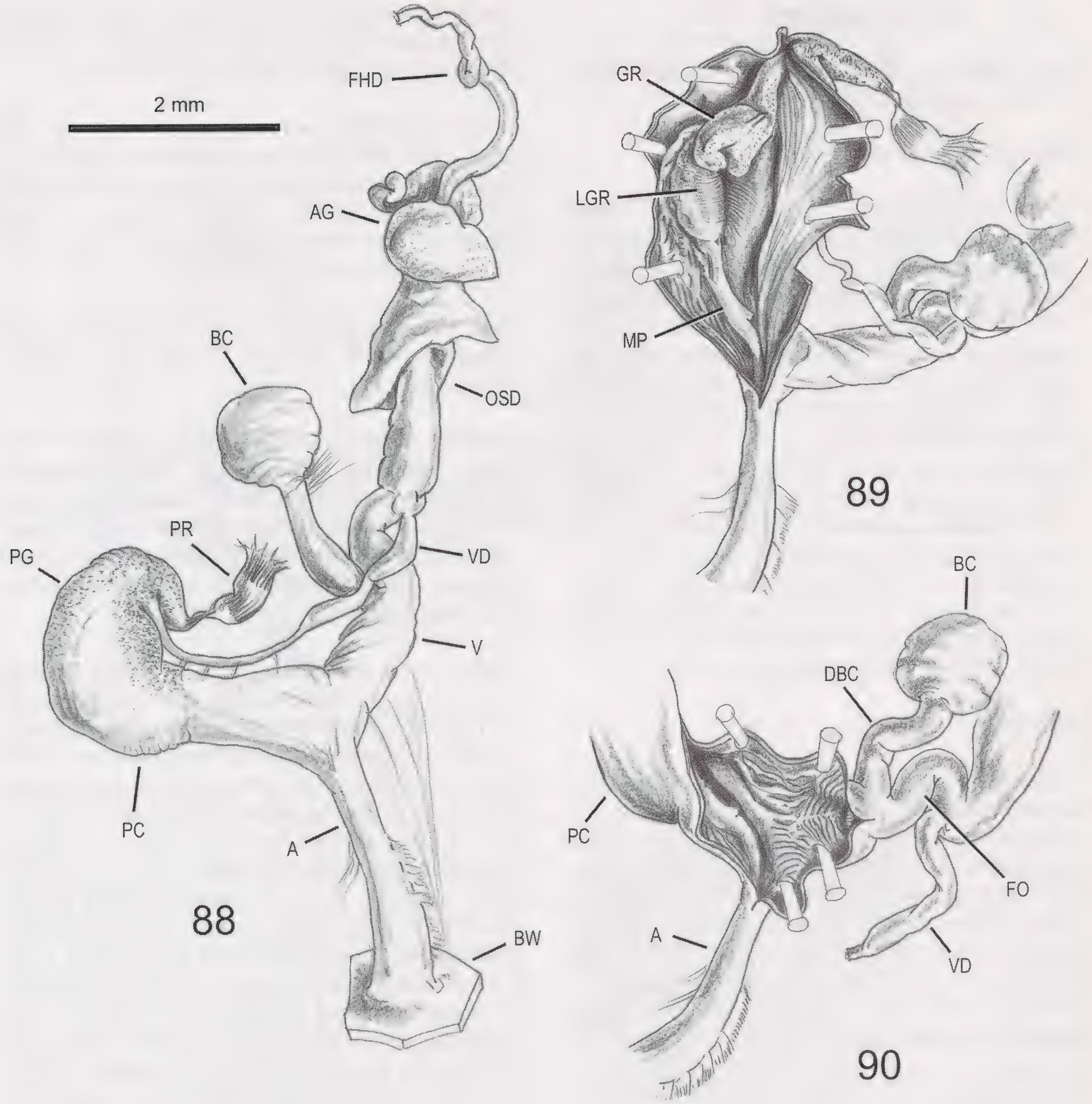
Remarks

Calidivitrina was established by Pilsbry (1919) as a new subgenus of *Vitrina*. Later it was considered a section of the subgenus *Vitrina (Vitrina)* by Thiele (1931), a junior synonym of *Vitrina (Vitrina)* by Hubendick (1953), a subgenus of *Semilimax* by Zilch (1959), a subgenus of *Vitrina* by Verdcourt (2005) and a distinct genus by Forcart (1978), Schileyko (1986) and Hausdorf (2002).

Hausdorf (2002) assigned eight species from Abyssinia, Kenya and Uganda to *Calidivitrina* (major anatomical references on which are: Hubendick, 1953; Forcart, 1957; Hausdorf, 2002; Schileyko, 2003) and regarded it as the sister group of *Arabivitrina*, and *Arabivitrina* plus *Calidivitrina* in turn the sister group of *Plutonia* plus *Oligolimax*.

The specimens dissected by us differ in some details with respect to those studied by Pilsbry (1919: 282–283, fig. 144c). They may therefore have been misidentified. However they were the only material available for our study.

Species assigned to *Calidivitrina* are relatively unknown because they have only



FIGS. 88–90. *Calidivitrina* cf. *oleosa* (Martens, 1895) from Cherangani near Kitale (Kenya), A. Jeannel leg. 10.3.1933. FIG. 88: Distal genitalia; FIG. 89: Internal structure of penial complex; FIG. 90: Vagina.

been summarily investigated, and there is no evidence that they constitute a monophyletic group. *Calidivitrina* includes Afrotropical vitrinids lacking a stimulator (glandula amatoria and diverticular stimulator), a feature shared by species such as *Eucobresia diaphana*, *Vitrina pellucida*, the Macaronesian *"Madeirovitrina" media* (Lowe, 1854) (cf. Groh & Hemmen, 1986) and *Azorivitrina brevispira* (Figs. 23, 24). *Vitrina pellucida* is distinct from all the others by virtue of different relationships between the right ommatophore retractor and the distal genitalia. *Arabivitrina brevispira* belongs to a genus endemic to the Azores on the basis of synapomorphic structure of the main pilaster. AP suggested that loss of the glandula amatoria happened at different times in different groups of vitrinids and that *Calidivitrina* belongs to a monophyletic clade together with *Guerrina* and *Madeirovitrina.* However, this clade must be considered with prudence because it is characterized by one non exclusive synapomorphy and may be biased by the fact that it was only possible to examine one species of *Calidivitrina* (two specimens: one adult already dissected and one juvenile).

Eucobresia Baker, 1929

Type Species: *Vitrina diaphana* Draparnaud, 1805, by original designation.

Material Examined

Eucobresia diaphana (Draparnaud, 1805) – Italy: Valtellina (Sondrio), 10.10.1952 (2 spirit specimens, FGC). Germany: Rheininsel Nonnenwerth (North Rhine-Westphalia), W. R. Schlickum leg. 17.11.1948 (2 spirit specimens, SMF 276318). Austria: Bregenzer Wald Damüls, Uga-Koft (Vorarlberg), H. Schönmann leg. 30.7.1973 (2 spirit specimens, NHMW 74317).

Eucobresia glacialis (Forbes, 1837) – Italy: Caverna della Gran Frana (Oulx, Torino), 32TLQ2893, S. Birindilli, E. Gavetti & E. Lana leg. 16.8.2000 (3 spirit specimens, FGC).

Eucobresia nivalis (Dumont & Mortillet, 1852) – Italy: Val Sesia, Col d'Olen (Alagna Valsesia, Vercelli), 32TMR1280, M. Bodon leg. 21.7.1990 (2 spirit specimens, FGC).

Diagnosis

Semislug-like vitrinids characterized by short penial retractor muscle arising from diaphragm, compelling penial complex below right ommatophore and in front of right optic nerve and ending on penial complex subapically (but juveniles with long penial retractor muscle running in front of right optic nerve, below right ommatophore retractor); stimulator absent; penial complex with penial gland and penial sheath; vas deferens contacting penial complex medially, traversing penial sheath, running along penial complex and entering it subapically; internal structures of penial complex comprising two distinctive pilasters, possibly homologous with main and accessory pilasters; larger pilaster (main pilaster?) consisting of presumably glandular, proximal portion and low, robust, medial-distal muscular pleat ending in genital atrium, having two transverse rows of fused thorn-like structures on one side of larger pilaster, at about half its length.

Description of Type Species

Shell: vitriniform very dilated, glossy, thin and fragile, depressed, with approximately 2.5 whorls; last whorl extremely expanded; aperture very wide with columellar and basal margins bordered by broad periostracal fringe; columellar margin slightly cut-away; umbilical area open; protoconch not prominent, smooth, with many regular spiral rows of very small pits; teleoconch smooth (Kerney & Cameron, 1979: pl. 7, fig. 1a–c).

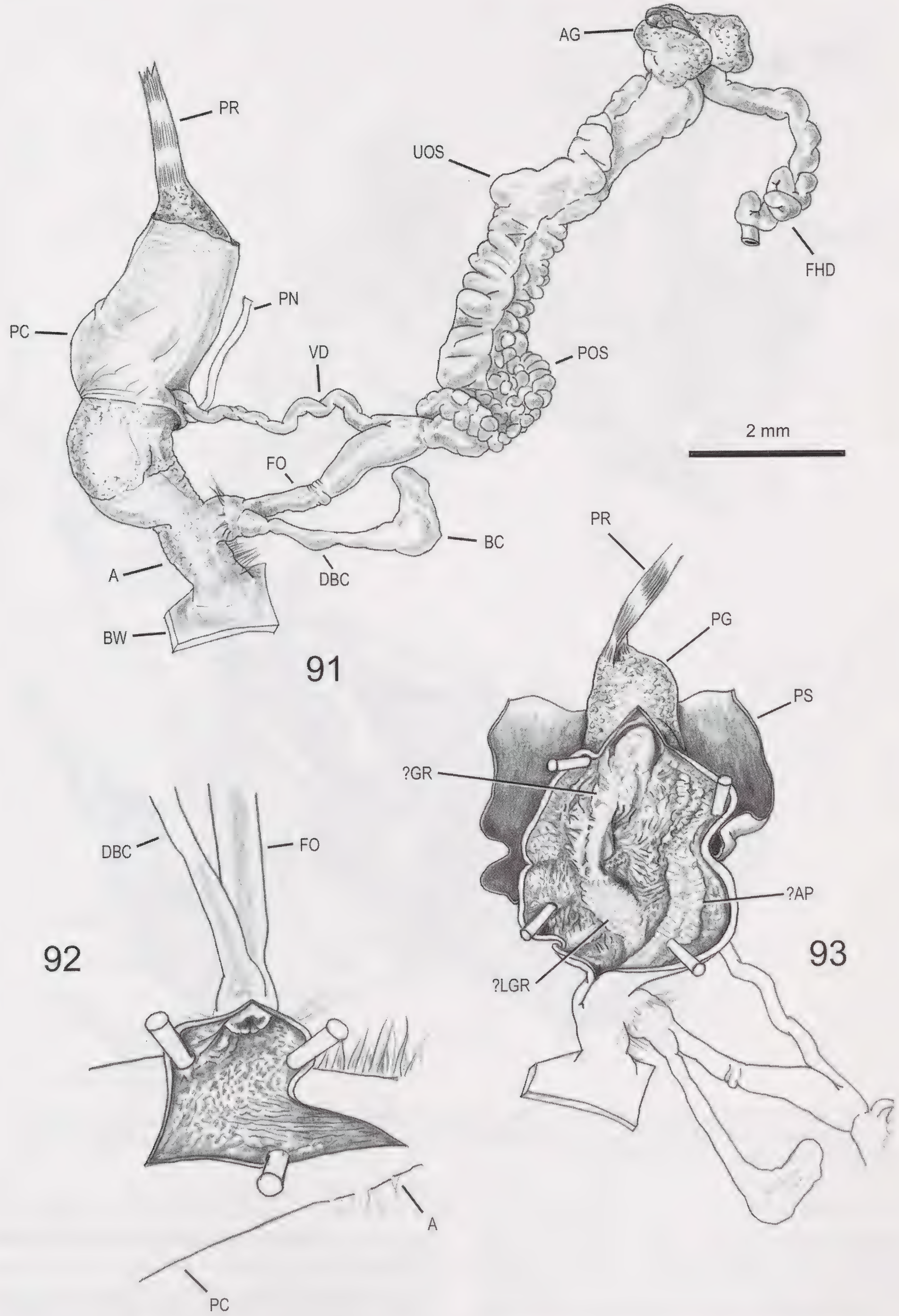
Body: cannot be withdrawn completely into shell; right shell lobe large, covering wide portion of shell when animal undisturbed (Kerney & Cameron, 1979: pl. 7, fig. 1d; Bogon, 1990: fig. at p. 183; Falkner, 1990: fig. 5 at p. 173; 1992: figs. 6–8 at p. 270).

Radula: dichoglossan; marginal teeth unicuspid (Wagner, 1915: 470, pl. 13, fig. 107; Hesse, 1923: 88).

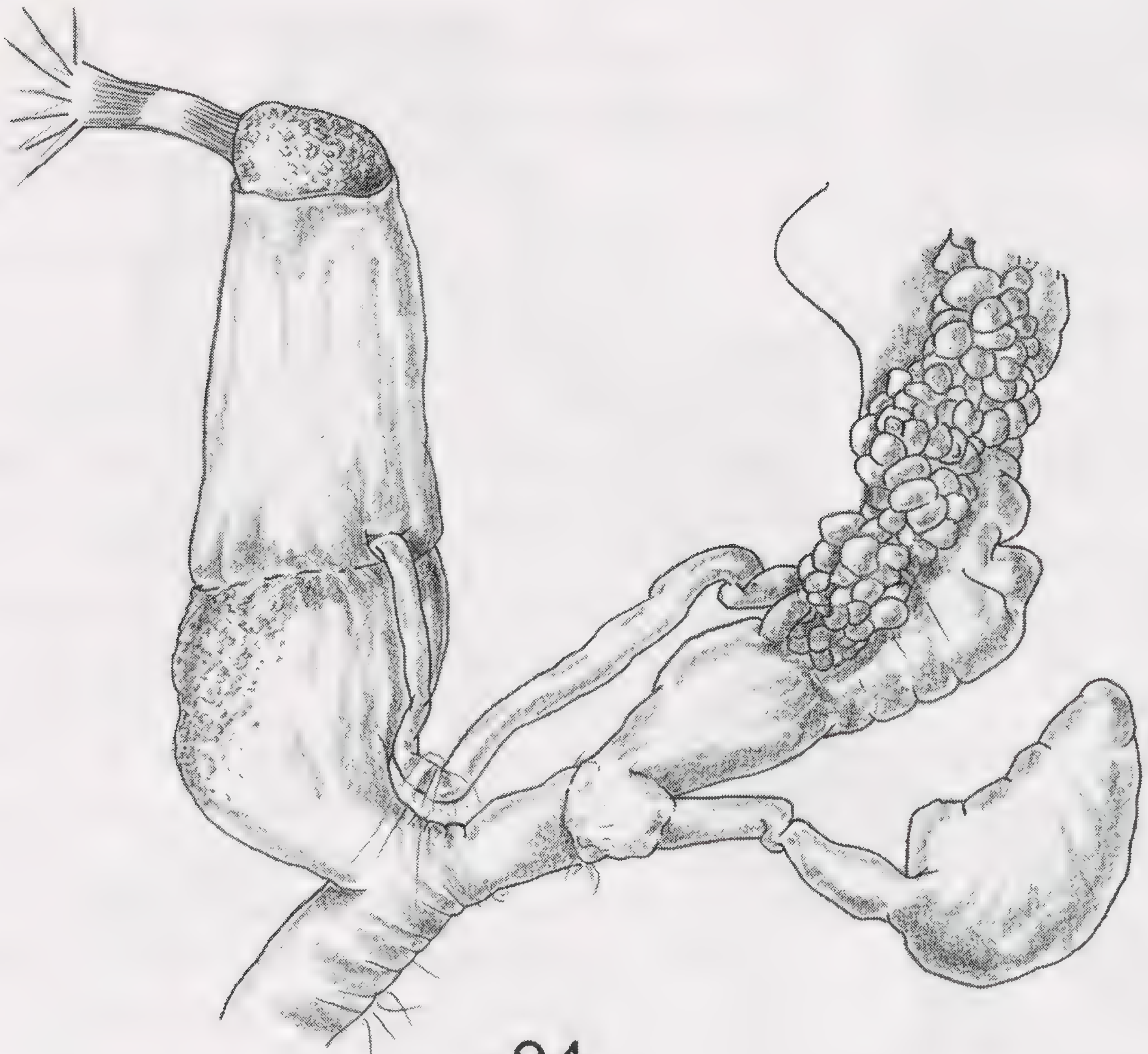
Female Distal Genitalia (Figs. 91–95): free oviduct short to long and wide. Bursa copulatrix small and oval to shoe-like in shape, with short to medium, more or less slender duct, initially not or only slightly flared. Vagina very short, without glandula amatoria but with internal proximal pad.

Male Distal Genitalia (Figs. 91–95): penial complex large and club-like, with penial gland and penial sheath. Penial gland covering most of penial complex. Penial sheath long, arising from mid penial complex and enveloping almost all proximal penial complex. Penial retractor arising from diaphragm, short, inserted apically. Vas deferens long (?), contacting penial complex medially, then traversing penial sheath, running along surface of penial gland and entering penial complex subapically near insertion of penial retractor. Internal structures of penial complex comprising two distinctive pilasters, possibly homologous with main and accessory pilasters. Larger pilaster (main pilaster?) consisting of presumably glandular proximal portion (modified glandular roll?) and low robust medial–distal muscular pleat ending in genital atrium (in one case muscular pleat gently transversely pleated before its final portion). One side of larger pilaster bearing two transversal rows of fused thorn-like structures at about half its length. Smaller pilaster (accessory pilaster?) arising level with medial portion of larger pilaster and ending in genital atrium. Vas deferens opening not visible, level with proximal penial complex, hidden by glandular tissue. Internal surface with thin irregularly arranged pleats and scattered spongy tissue with crypts.

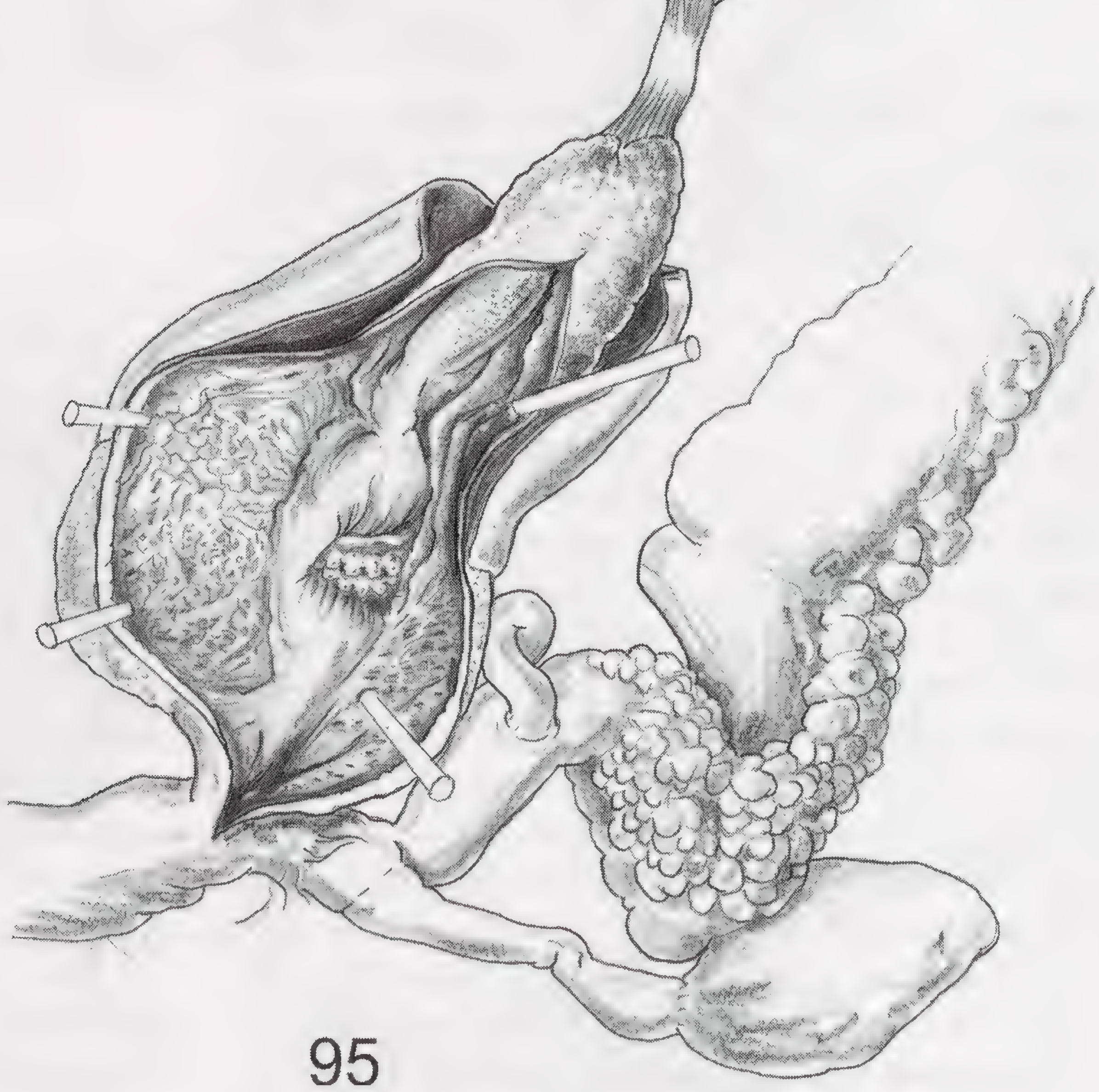
Genital Atrium (Figs. 91–95): short, with one side connected to body wall by thin muscular bands. Internal surface as in penial complex.



FIGS. 91–93. *Eucobresia diaphana* (Draparnaud, 1805) from Valtellina (Lombardy, Italy), 10.10.1952. FIG. 91: Distal genitalia; FIG. 92: Internal structure of genital atrium; FIG. 93: Penial complex.



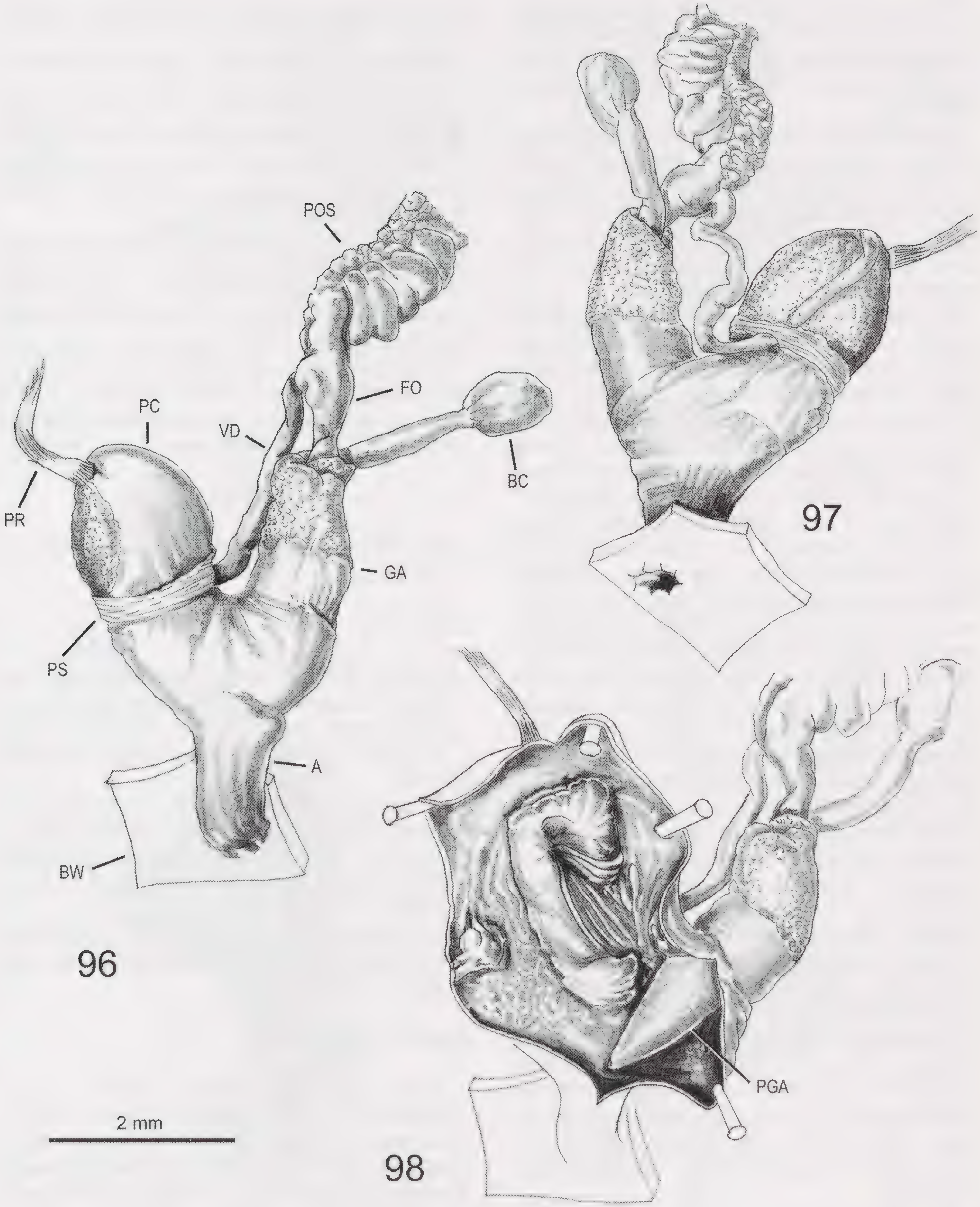
94



95

FIGS. 94, 95. *Eucobresia diaphana* (Draparnaud, 1805) from Rheininsel Nonnenwerth (North Rhine-Westphalia, Germany), W. R. Schlickum leg. 17.11.1948. FIG. 94: Distal genitalia; FIG. 95: Internal structure of penial complex.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: age-dependent (Fig. 5). Juveniles with long slender penial retractor passing below right ommatophore and in front of right optic nerve; distal genitalia lying right of right ommatophore retractor which therefore appears free of penial complex and vagina. Adults with penial retractor short so that penial complex more or less is below right ommatophore and in front of right optic nerve; right ommatophore is consequently shifted right and compelled to lie between penial complex and vagina.



FIGS. 96–98. *Eucobresia glacialis* (Forbes, 1837) from Caverna della Gran Frana (Piedmont, Italy), S. Birindilli, E. Gavetti & E. Lana leg. 16.8.2000. FIGS. 96, 97: Distal genitalia; FIG. 98: Internal structure of penial complex and distal vagina.

Mating: described by Gerhardt (1936). Stimulator is not used for fixing partner and penis is inserted into vagina or duct of bursa copulatrix during copulation.

Remarks

Eucobresia was introduced by Baker (1929) as a new name for *Semilimax sensu* Hesse, 1923 (*non* Stabile, 1859). Later, it was regarded as a section of the subgenus *Vitrina (Vitrina)* and subsequently as a distinct genus by all authors (Forcart, 1944; Zilch, 1959; Schileyko, 1986; etc.).

According to Hausdorf (2002), *Eucobresia* includes four species from the Alps, Balkan Peninsula, central Europe and western Europe (major anatomical references: Forcart, 1944; Schileyko, 1986; Hausdorf, 2002) and is the sister group of (*Phenacolimax* ((*Plutonia*, *Oligolimax*) (*Arabivitrina*, *Calidivitrina*))).

Eucobresia diaphana has a very short, simple vagina without glandula amatoria but with a simple internal proximal pad, matching that described by Schileyko (1986: fig. 12B). On the contrary, Hausdorf (2002) stated that *Eucobresia* had a glandula amatoria without external glandular layer (which he considered an autapomorphy of this genus; Hausdorf, 2002: note 2 at p. 358). It is evident that he based this statement not on the type species but on another species (namely *E. glacialis*), which he supposed to belong to *Eucobresia* because it was characterized by the penial sheath and the right ommatophore retractor between penial complex and vagina. This species was redescribed by Forcart (1944) and assigned by him to *Insulivitrina* on the basis of the right ommatophore retractor being free of the distal genitalia, but Hausdorf (2002: note 2 at p. 358) sustained that Forcart was wrong.

According to Hausdorf (2002), *Eucobresia* included two other species, *E. nivalis* and *E. pegorarii* (Pollonera, 1884), besides the type species and *E. glacialis*. Unfortunately, the identity of the species assigned to *Eucobresia* is problematical because revisions have been performed without considering typical or topotypical material, and their relationships are still uncertain pending meticolous anatomical studies. For example, in disagreement with Hausdorf, *E. glacialis* has a glandula amatoria with external glandular covering, albeit incomplete (Figs. 96–98). We therefore limited the diagnosis of the genus to the characters of *E. diaphana*.

The other species included in *Eucobresia*, as they are currently conceived, have shells with columellar margin not cut-away and lack the two transverse crests of fused thorn-like structures inside the penial complex (these characters may be only species-specific: shells with columellar margin cut-away are found in other vitrinids, such as some Macaronesian species and some *Semilimax*). Apart from *E. glacialis*, the other species are characterized by progressive reduction of muscular section of glandula amatoria to an annular pad. For example, *E. nivalis* has a general scheme of the genitalia rather similar to that of *E. diaphana* but is distinguished by the fact that the vagina contains a rather well developed conical papilla which resembles that of a typical glandula amatoria, although there is no glandula amatoria (Figs. 99–102).

The vaginal pad of *E. diaphana* may be an extreme stage of reduction of the glandula amatoria of a *Phenacolimax*-like ancestor that went through stages exemplified by *E. glacialis* and then *E. nivalis*. Although we investigated this hypothesis considering three species of *Eucobresia* and two of *Phenacolimax* in the phylogenetic analysis, a clade including all five or at least some of them was not recovered.

Vitrina Draparnaud, 1801

Type Species: *Helix pellucida* Müller, 1774, by monotypy.

Synonyms

Cobresia Hübner, 1810. Type Species: *Cobresia vitrea* Hübner, 1810, by subsequent designation (Baker, 1929). *Cobresia vitrea* is a junior synonym of *Helix pellucida* Müller, 1774.

Helicolimax Férussac, 1801. Type Species: *Helix pellucida* Müller, 1774, by monotypy.

? *Hyalina* Studer, 1820, *non* Schumacher, 1817. Type designation not traced (Barker, 1999).

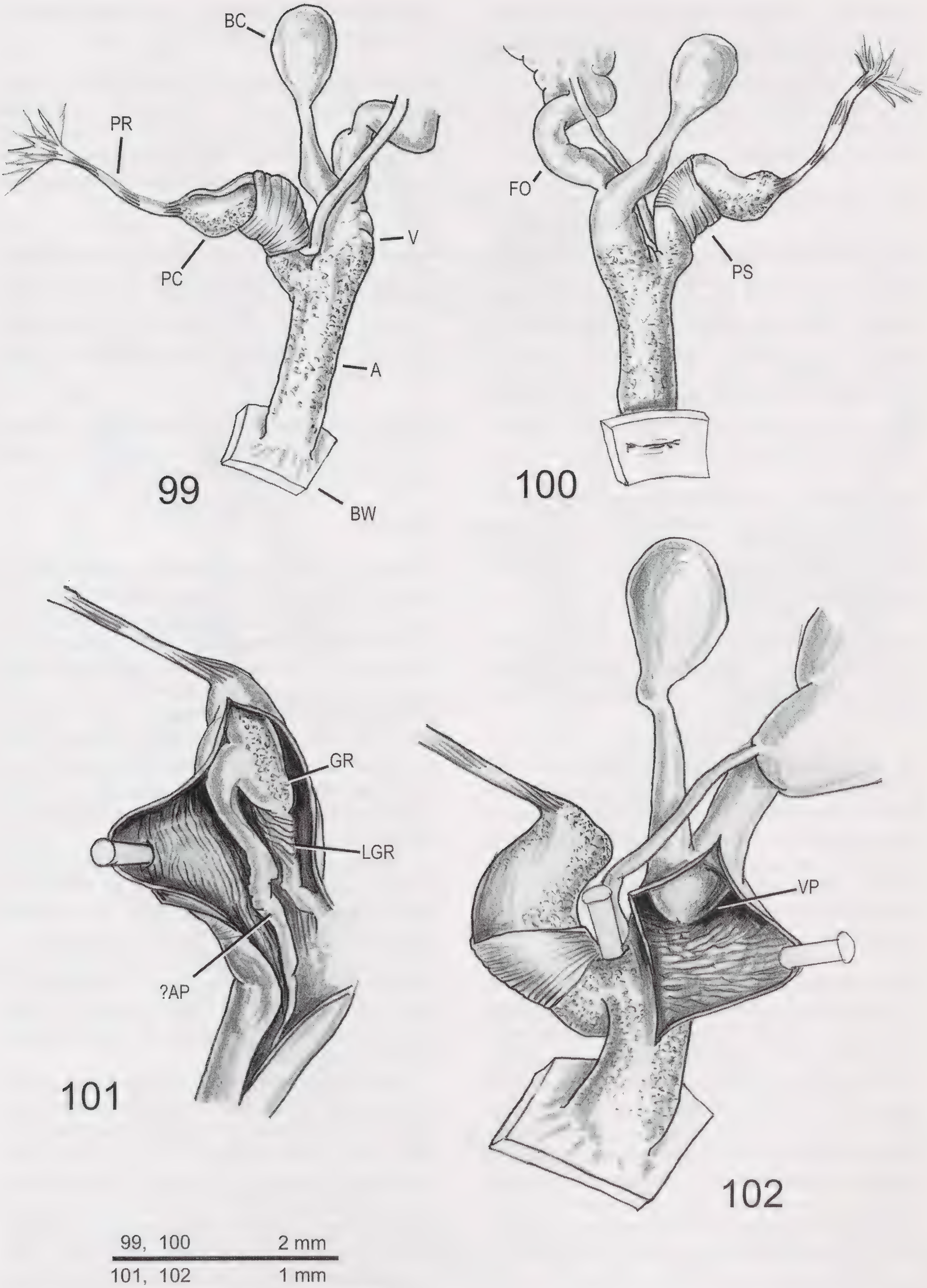
Pagana Gistl, 1847. Type Species: *Helix pellucida* Müller, 1774, by subsequent designation (Baker, 1929).

Material Examined

Vitrina pellucida (Müller, 1774) – Italy: Gasperone (Vernio, Prato), 32TPP7185, S. Cianfanelli & E. Lori leg. 30.10.2002 (1 spirit specimen, FGC). Bossea (Frabosa Soprana, Cuneo), M. Bodon leg. 9.4.1987 (1 spirit specimen, FGC). United Kingdom: Dollar Glen (Scotland), F. Giusti & G. Manganelli leg. 3.9.1986 (5 spirit specimens, FGC).

Diagnosis

Semislug-like vitrinids characterized by long penial retractor muscle arising from diaphragm, passing above right ommatophore retractor and ending on penial complex subapically; stimula-



FIGS. 99–102. *Eucobresia nivalis* (Dumont & Mortillet, 1852) from Val Sesia, Col d'Olen (Piedmont, Italy), M. Bodon leg. 21.7.1990. FIGS. 99, 100: Distal genitalia; FIG. 101: Internal structure of penial complex; FIG. 102: Distal vagina.

tor absent; penial complex with penial gland and penial sheath; vas deferens contacting penial complex distally, traversing penial sheath, running along penial complex and entering it apically; internal structures of penial complex comprising only main pilaster consisting of slender, not distally lamellate, glandular roll.

Description of Type Species

Shell: vitriniform typical, glossy, thin and fragile, globular-depressed, with approximately 3.0 whorls; last whorl expanded; aperture moderately wide with basal margin bordered by narrow periostracal fringe; columellar margin normal; umbilicus open, punctiform; protoconch not prominent, smooth, with many regular spiral rows of very small pits; teleoconch smooth (Kerney & Cameron, 1979: pl. 6, fig. 1a–c).

Body: cannot be withdrawn completely into shell; right shell lobe small, covering very limited portion of shell when animal undisturbed (Kerney & Cameron, 1979: pl. 6, fig. 1d; Falkner, 1990: fig. 1 at p. 173).

Radula: dichoglossan; marginal teeth pluricuspid (Taylor, 1906: 6, figs. 8, 9; Wagner, 1915: 471, pl. 13, fig. 95; Castillejo, 1985: 66, fig. 1).

Female Distal Genitalia (Figs. 103–105): free oviduct short and wide. Bursa copulatrix medium in size and sac-like with short, more or less slender duct, initially very flared. Vagina very short, without glandula amatoria or other internal structures, but with external glandular covering also on initial part of duct of bursa copulatrix.

Male Distal Genitalia (Figs. 103–105): penial complex small and finger-like, with penial gland and penial sheath. Penial gland covering most of penial complex. Penial sheath long, sometimes curled up, arising from end of penial complex and enveloping almost all penial complex. Penial retractor arising from diaphragm, long, inserted apically. Vas deferens long, contacting penial complex distally, then traversing penial sheath, running along surface of penial gland and entering penial complex apically near insertion of penial retractor. Internal structures of penial complex comprising main pilaster only, which consists of slender glandular roll not distally lamellate, ending before genital atrium. Vas deferens opening not visible, probably level with initial part of glandular roll. Internal surface with sparse spongy tissue with crypts.

Genital Atrium (Figs. 103–105): long to very long and cylindrical, with sparse glandular covering (in close continuity with that on vagina) and opposite sides connected to body wall by thin muscular bands. Internal surface with low pleats.

Relationships Between Right Ommatophore Retractor and Distal Genitalia: similar in juveniles and adults (Fig. 10). Penial retractor long, passing above right ommatophore retractor which is consequently free of penial complex and vagina.

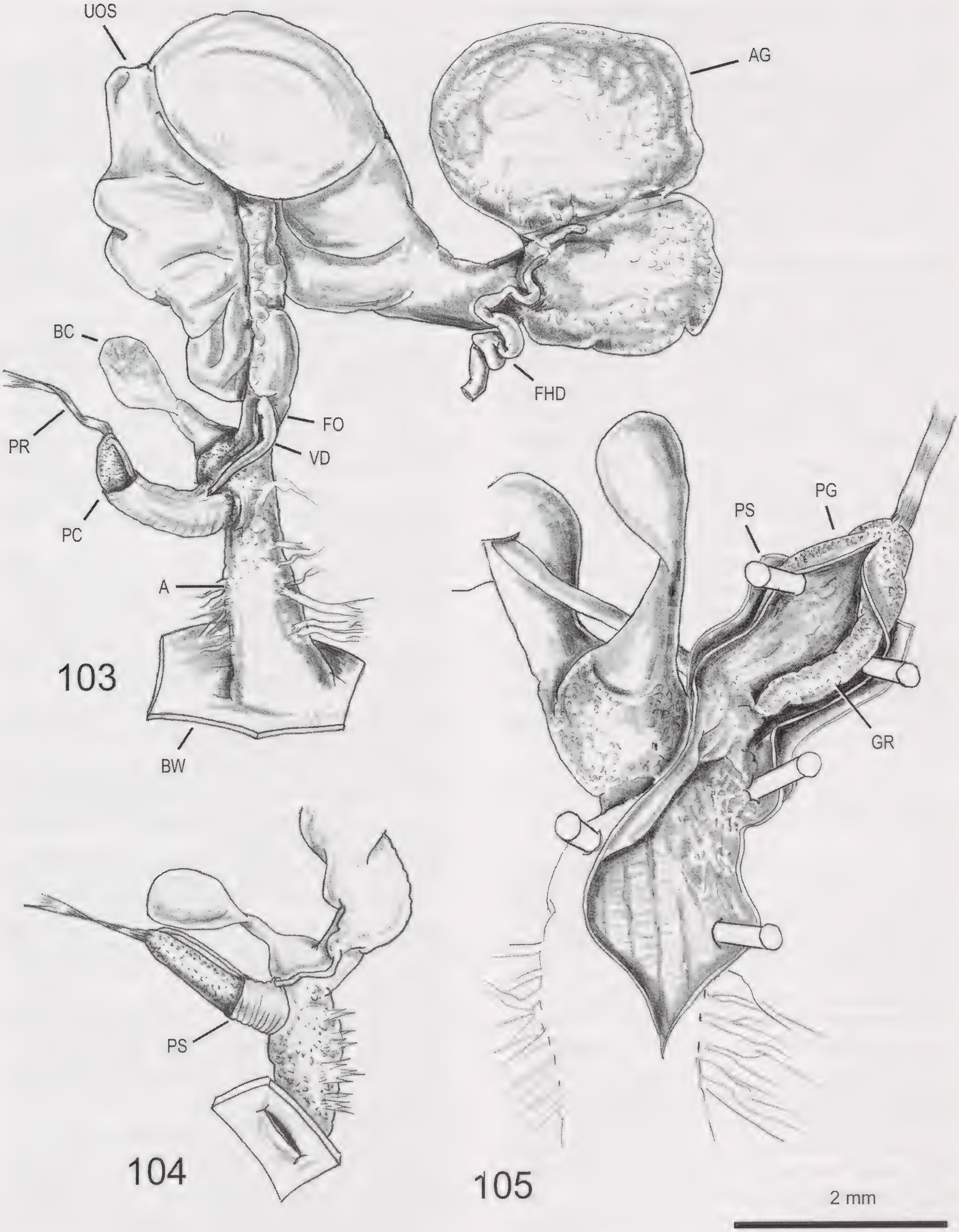
Mating: Hausdorf (2002) stated that in *Vitrina*, penis is inserted in vagina or duct of bursa copulatrix during copulation.

Remarks

Vitrina is the first genus-group taxon established for this group of land pulmonates. The genus has Holoarctic distribution and according to Hausdorf (2002) includes only three anatomically known species (major anatomical references on which are: Eckardt, 1914 [not seen; fide Hausdorf (2002)]; Pilsbry, 1946; Forcart, 1955; Umiński, 1968; Schileyko, 1986, 2003) and is the sister group of *Semilimacella*; in turn *Semilimacella* plus *Vitrina* is sister group of (*Eucobresia* (*Phenacolimax* ((*Plutonia*, *Oligolimax*) (*Arabivitrina*, *Calidivitrina*)))).

In disagreement with Hausdorf (1995, 2002) and Schileyko (2003), we are of the same opinion as Lohmander (1938), that *Vitrina pellucida* has a vagina, though very short. Its presence is confirmed by the fact that in adult specimens its walls (like those of initial part of duct of bursa copulatrix) are covered by glandular tissue (like in species of *Semilimacella* and oxychiline zonitids).

The other anatomically known species are *V. angelicae* Beck, 1837, from Greenland and North America and *Vitrina rugulosa* Martens, 1874, from Asian Russia. Although these species share the same scheme of the genitalia, they apparently differ in important details and it is therefore unclear whether they constitute a monophyletic group together with *V. pellucida*. *V. angelicae* differs from *V. pellucida* by virtue of duct of bursa copulatrix initially not flared and absence of penial sheath (for anatomy: Soós & Schlesch, 1924; Forcart, 1955). *V. rugulosa* dif-



FIGS. 103–105. Distal genitalia of specimens of *Vitrina pellucida* (Müller, 1774). FIGS. 103, 105: Specimen from Gasperone (Tuscany, Italy), S. Cianfanelli & E. Lori leg. 30.10.2002; FIG. 104: Specimen from Bossea (Piedmont, Italy), M. Bodon leg. 9.4.1987.

fers from *V. pellucida* by virtue of duct of bursa copulatrix initially not flared and pad bordering opening of duct of bursa copulatrix into vagina (for anatomy: Schileyko, 1986).

AP (DPIII) suggested that *V. pellucida* forms a monophyletic group with *Semilimacella bonelli* (61% symmetric resampling, 0.22/67 absolute and relative Bremer supports) on the basis of at least one synapomorphy (bursa copulatrix duct initially very flared). Moreover, MP and AP showed that these two species belong to a larger monophyletic group having very low support (MP: 50%; AP: 9% symmetric resampling, 0.15/40 absolute and relative Bremer supports) including four other species (*Oligolimax annularis*, *O. musignani*, *Sardovitrina polloneriana* and *Semilimacella cephalonica*) based on exclusive disposition of penial retractor above right ommatophore retractor. Relationships between *V. pellucida* and the vitrinids with atrial-vaginal stimulator are not new. Indeed, Umiński (1968) described a small diverticulum located on the proximal atrium opposite the penial complex in juveniles of *Vitrina pellucida*. He compared it with the atrial stimulator of *Hessemilimax kotulae* and in the absence of definitive evidence about homology of the two structures, he concluded that the small atrial diverticulum of *Vitrina pellucida* is probably a vestige of an atrial stimulator.

ACKNOWLEDGEMENTS

We thank Simone Cianfanelli (Florence, Italy), Maria del Rosario Alonso (La Laguna, Canary Is., Spain), Marco Bodon (Genoa, Italy), Gianni Comotti (Bergamo, Italy), António Manuel de Frias Martins (Ponta Delgada, Azores, Portugal), Elena Gavetti (Turin, Italy), Klaus Groh (Hackenheim, Germany), Alessandro Minelli (Padua, Italy) and Jos Nienhuis (Woltersum, The Netherlands) for field collection or loan of material, Thierry Backeljau (Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium), Anita Eschner (Naturhistorisches Museum Wien, Vienna, Austria), Virginie Héros (Muséum National d'Histoire Naturelle, Paris, France), Ronald Janssen (Senckenberg-Museum, Frankfurt am Main, Germany) and Anatoly Schileyko (Zoological Museum of Moscow University, Moscow, Russia) for information about or loan of material from collections of their respective museums and Helen Ampt for revising the English.

LITERATURE CITED

ALONSO, M. R., M. IBÁÑEZ & P. MORALES, 1987, La familia Vitrinidae en Canarias. II. Revisión de las especies de La Palma y El Hierro, con descripción de una especie nueva (Gastropoda: Pulmonata). *Archiv für Molluskenkunde*, 118(1–3): 63–76.

ALONSO, M. R., M. J. VALIDO, K. GROH & M. IBÁÑEZ, 2000, *Plutonia (Canarivitrina)*, new subgenus, from the Canary Islands, and the phylogenetic relationships of the subfamily Plutoniinae (Gastropoda: Limacoidea: Vitrinidae). *Malacologia*, 42(1–2): 39–62.

BACKHUYS, W., 1975, *Zoogeography and taxonomy of the land and freshwater molluscs of the Azores*. Backhuys & Meesters, Amsterdam, XII + 350 pp., 97 maps, 32 pls.

BAKER, H. B., 1929, Nomenclature in the genus *Vitrina*. *The Nautilus*, 42(4): 137–139.

BANK, R. A., P. BOUCHET, G. FALKNER, E. GITTENBERGER, B. HAUSDORF, T. VON PROSCHWITZ & Th. E. J. RIPKEN, 2001, Supraspecific classification of European non marine Mollusca (CLECOM Sections I + II). *Heldia*, 4(1–2): 77–128.

BANK, R. A., K. GROH & T. E. J. RIPKEN, 2002, Catalogue and bibliography of the non-marine Mollusca of Macaronesia. Pp. 89–235, pls. 14–26, in: M. FALKNER, K. GROH & M. C. D. SPEIGHT, eds., *Collectanea Malacologica. Festschrift für Gerhard Falkner.* ConchBooks/Friedrich-Held-Gesellschaft, Hackenheim/München.

BARKER, G. M., 1999, Naturalised terrestrial Stylommatophora (Mollusca: Gastropoda). *Fauna of New Zealand*, 38: 1–254.

BOATO, A., M. BODON & F. GIUSTI, 1986, Molluschi terrestri e d'acqua dolce delle Alpi Liguri. *Lavori della Società Italiana di Biogeografia, Nuova Serie*, 9: 237–371.

BOETTGER, O., 1880, Diagnoses molluscorum novorum ab ill. Hans Leder in regione caspia Talysch lectorum. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft*, 7: 379–383.

BOGON, K., 1990, *Landschnecken. Biologie, Ökologie, Biotopschutz*. Natur-Verlag, Augsburg, 404 pp.

BOYCOTT, A. E., 1914, A note on the anatomy of the Irish *Vitrina* described as *V. pyrenaica* or *V. hibernica*. *The Irish Naturalist*, 23: 205–209.

CASTILLEJO, J., 1985, Caracoles terrestres de Galicia, II. Familia Zonitidae (Gastropoda Pulmonata). *Iberus*, 5: 63–81.

DAMJANOV, S. G. & I. M. LIKHAREV, 1975, Gastropoda Terrestria. *Fauna Bulgarica*, 4: 1–426.

DAVISON, A. & P. MORDAN, 2005, A literature database on the mating behaviour of stylommatophoran land snails and slugs. *American Malacological Union*, 23(1): 173–181.

DE WINTER, A. J., 1990, Little known land snails from the French Alps (Pulmonata). *Basteria*, 54(4–6): 227–237.

ECKARDT, E., 1914, Beiträge zur Kenntnis der einheimischen Vitrinen. *Jenaische Zeitschrift für Naturwissenschaften*, 51: 213–376, pl. 4.

FALKNER, G., 1990, Binnenmollusken. Pp. 112–273, in: R. Fechter & G. Falkner, *Weichtiere. Europäische Meeres- und Binnenmollusken*. Mosaik-Verlag, München.

FALKNER, G., 1992, Binnenschnecken und Süßwassermuscheln. Pp. 238–321, in: J. H. Reichholf & G. Steinbach, eds., *Die große Bertelsmann-Lexikothek, Naturenzyklopädie Europas, 6 (Mollusken und andere Wirbellose)*. Mosaik-Verlag, München.

FARRIS, J. S., 1988, *Hennig86. Program and documentation*. Port Jefferson Station, New York.

FORCART, L., 1944, Monographie der schweizerischen Vitrinidae (Moll. Pulm.). *Revue Suisse de Zoologie*, 51(29): 629–678, pls. 1–2.

FORCART, L., 1949, Die Erektion der Kopulationsorgane und der Kopulationsmodus von *Phenacolimax major* (Fer.). *Archiv für Molluskenkunde*, 77(1–6): 115–119.

FORCART, L., 1955, Die nordischen Arten der Gattung *Vitrina*. *Archiv für Molluskenkunde*, 84(4–6): 155–166.

FORCART, L., 1956, Die Vitrinidae der Ostalpen. *Archiv für Molluskenkunde*, 85(1–3): 1–14, pl. 1.

FORCART, L., 1957, Die Vitrinidae von Baden (Moll., Styl.). *Mitteilungen des Badischen Landesvereins fuer Naturkunde und Naturschutz*, 7(1): 19–24.

FORCART, L., 1959, Revision nordafrikanischer Vitrinidae. *Archiv für Molluskenkunde*, 88(1–3): 1–6, pl. 1.

FORCART, L., 1960, Mollusken aus den Abruzzen mit taxonomischen Revisionen und anatomischen Beschreibungen. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 71 (1): 125–139.

FORCART, L., 1965, Rezente Land- und Süsswassermollusken der süditalienischen Landschaften Apulien, Basilicata und Calabrien. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 76(1): 59–184.

FORCART, L., 1978, African distribution of genera and subgenera of the family Vitrinidae (Pulmonata). *Journal of Conchology*, 29(6): 325–327.

GAVETTI, E., S. BIRINDELLI, M. BODON & G. MANGANELLI, 2008, Molluschi terrestri e d'acqua dolce della Valle di Susa. *Museo Regionale di Scienze Naturali (Turin), Monografie*, 44: 1–273.

GERHARDT, U., 1936, Weitere Untersuchungen zur Kopulation der Stylommatophoren. *Zeitschrift für Morphologie und Ökologie der Tiere*, 31: 433–442.

GERMAIN, L., 1930, Mollusques terrestres et fluviatiles. Première partie. *Faune de France*, 21: 1–477 + i–viii, pls. 1–13. Lechevalier, Paris.

GIUSTI, F., 1973, Notulae Malacologicae XVI. I Molluschi terrestri e di acqua dolce viventi sul massiccio dei Monti Reatini (Appennino Centrale). *Lavori della Società Italiana di Biogeografia, Nuova Serie*, 2: 423–576, 7 pls.

GIUSTI, F., L. CASTAGNOLO & G. MANGANELLI, 1985, La fauna malacologica delle faggete italiane: brevi cenni di ecologia, elenco delle specie e chiavi per il riconoscimento dei generi e delle entità più comuni. *Bollettino Malacologico*, 21(5–6): 69–144.

GIUSTI, F. & M. MAZZINI, 1971, Notulae Malacologicae XIV. I Molluschi delle Alpi Apuane. Elenco delle specie viventi con descrizione di una nuova specie: *Vitrinobrachium baccettii* n. sp. *Lavori della Società Italiana di Biogeografia, Nuova Serie*, 1: 202–335, 9 pls.

GOLOBOFF, P. A., 1993, Estimating character weights during tree search. *Cladistics*, 9: 83–91.

GOLOBOFF, P. A., 1995, Parsimony and weighting: a reply to Turner and Zandee. *Cladistics*, 11: 91–104.

GOLOBOFF, P. A. & J. S. FARRIS, 2001, Methods for quick consensus estimation. *Cladistics*, 17: S26–S34.

GOLOBOFF, P. A., J. S. FARRIS & K. NIXON, 2003, *TNT (Tree analysis using New Technology), Version 1.0.* Published by the authors, Tucumán.

GROH, K. & J. HEMMEN, 1986, Zur Kenntnis der Vitriniden des Madeira-Archipels (Pulmonata: Vitrinidae). *Archiv für Molluskenkunde*, 116(4–6): 183–217.

HAUSDORF, B., 1995, The Vitrinidae of Turkey, with remarks on the phylogeny of *Gallandia* (Gastropoda: Stylommatophora). *Zoologischer Anzeiger*, 234(1): 63–74.

HAUSDORF, B., 1998, Phylogeny of the Limacoidea *sensu lato* (Gastropoda: Stylommatophora). *Journal of Molluscan Studies*, 64(1): 35–66.

HAUSDORF, B., 2002, Phylogeny and biogeography of the Vitrinidae (Gastropoda: Stylommatophora). *Zoological Journal*, 134(3): 347–358.

HESSE, P., 1923, Beiträge zur näheren Kenntnis der Familie Vitrinidae. *Archiv für Molluskenkunde*, 55(1–2): 1–25, pls. 1–2, (3): 81–115, (4): 129–145.

HESSE, P., 1924, Kritische Fragmente. *Archiv für Molluskenkunde*, 56(4): 226–230.

HOFFMANN, H., 1929, Die Vitrinen der Atlantischen Inseln. *Senckenbergiana*, 11(4): 218–235.

HUBENDICK, B., 1953, The relationships of the East African *Vitrinae* with notes on the taxonomy of *Vitrina*. *Arkiv för Zoologi, Serie 2*, 6(5): 83–96.

HUELSENBECK, J. P. & F. RONQUIST, 2001, MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17(8): 754–755.

IBÁÑEZ, M., M. R. ALONSO & M. J. VALIDO, 2001, *Plutonia solemi* new species (Gastropoda: Vitrinidae: Plutoniinae) from La Palma (Canary Islands). *Journal of Conchology*, 37(2): 149–157.

IBÁÑEZ, M., P. MORALES & M. R. ALONSO, 1987, La familia Vitrinidae en Canarias. I. Revisión de las especies de Tenerife, con descripción de 2 especies nuevas (Gastropoda: Pulmonata). *Archiv für Molluskenkunde*, 117(4–6): 117–149.

JUNGBLUTH, J. H., I. M. LIKHAREV & A. WIKTOR, 1985, Vergleichend morphologische

Untersuchungen an der Radula der Landnacktschnecken. II. Arionoidea und Trigonochlamydoidea (Gastropoda: Pulmonata). *Archiv für Molluskenkunde*, 116(1–3): 25–45, pls. 1–4.

KASS, R. E. & A. E. RAFTERY, 1995, Bayes factors. *Journal of the American Statistical Association*, 90(430): 773–795.

KERNEY, M. P. & R. A. D. CAMERON, 1979, *A field guide to the land snails of Britain and northwest Europe*. Collins, London, 288 pp., 24 pls.

KÜNKEL, K., 1929, Experimentelle Studie über *Vitrina brevis* Fér. *Zoologische Jahrbücher, Abteilung für Allgemeine Zoologie und Physiologie der Tiere*, 46: 575–626.

KÜNKEL, K., 1933, Vergleichende experimentelle Studie über *Vitrina elongata* Draparnaud und *Vitrina brevis* Férussac. *Zoologische Jahrbücher, Abteilung für Allgemeine Zoologie und Physiologie der Tiere*, 52: 399–432, pls. 5–7.

LEWIS, P. O., 2001, A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, 50(6): 913–925.

LOHMANDER, H., 1938, Landmollusken aus Island gesammelt von Dr. C. H. Lindroth (1929). *Göteborgs Kungliga Vetenskaps och Vitter Hetssamhalles Handlingar Sjatte Foljden Series B*, 6: 1–52, pls. 1–4.

MANGANELLI, G., M. BODON, L. FAVILLI & F. GIUSTI, 1995, Gastropoda Pulmonata. Pp. 1–60, in: A. MINELLI, S. RUFFO & S. LA POSTA, eds., *Checklist delle specie della fauna d'Italia*, 16. Edizioni Calderini, Bologna.

MANGANELLI, G. & F. GIUSTI, 2004, Status and relationships of *Vitrina musignani* Pirajno, 1842, and *Vitrina paulucciae* Fischer in Paulucci, 1878 (Gastropoda: Pulmonata: Vitrinidae). *Journal of Conchology*, 38(3): 291–304.

MANGANELLI, G. & F. GIUSTI, 2005, The status and relationships of *Vitrina polloneriana* Fra' Piero, 1897, with description of *Sardovitrina* n. gen. (Gastropoda: Pulmonata: Vitrinidae). *Journal of Conchology*, 38(5): 567–579.

MARTENS, E. VON, 1895, Neue Arten von Landschnecken aus den Gebirgen Ost-Afrikas. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*, 18 Juni 1895: 120–129.

MEDEIROS, R., C. BRITO, A. M. DE FRIAS MARTINS, K. JORDAENS, P. VAN RIEL, H. DE WOLF, K. BREUGELMANS & T. BACKELJAU, 2000, Conservation genetics of the endemic Azorean slug *Plutonia atlantica* (Morelet, 1860) (Mollusca, Pulmonata). *Conservation Biology*, 93: 77–84.

MILDNER, P., 1982, Die Molluskensammlung im Landesmuseum für Kärnten. *Kärntner Museumsschriften*, 69: 1–72, pls. 1–8.

MOQUIN TANDON, A., 1855–1856, *Histoire naturelle des Mollusques terrestres et fluviatiles de France, contenant des études générales sur leur anatomie et leur physiologie et la description particulière des genres, des espèces et des varietés*. J.-B. Baillière, Paris, 1: I–VIII + 1–416 pp. (1855), 2: 1–646 pp. (1856), Atlas: 1–92 pp., 1–54 pls. (date of publication unknown).

MORALES, P., M. IBÁÑEZ & M. R. ALONSO, 1988, La familia Vitrinidae en Canarias. III. Tres nuevas especies de la Gomera (Gastropoda: Pulmonata). *Archiv für Molluskenkunde*, 118(1–3): 153–166.

MORDAN, P. B. & A. M. F. MARTINS, 2001, A systematic revision of the vitrinid semislugs of the Azores (Gastropoda: Pulmonata). *Journal of Molluscan Studies*, 67(3): 343–368.

MURATOV, I. V., 1999, Analysis of the phylogenetic relationships and their systematic implications in the Limacoinei (= Zonitinia) infraorder (Gastropoda, Pulmonata, Geophila). *Ruthenica*, 9(1): 5–26.

NARDI, G., I. NIERO & A. BRACCIA, 2007, Nota sui Vitrinidae (Gastropoda, Pulmonata) viventi in provincia di Brescia. *Natura Bresciana*, 35: 101–119.

NEUBERT, E., 1998, Annotated checklist of the terrestrial and freshwater molluscs of the Arabian Peninsula with descriptions of new species. *Fauna of Saudi Arabia*, 17: 333–461.

NYLANDER, J. A. A., F. RONQUIST, J. P. HUELSENBECK & J. L. NIEVES, 2004, Bayesian phylogenetic analysis of combined data. *Systematic Biology*, 53(1): 47–67.

ODHNER, N. H., 1937, Little-known land Mollusca from Madeira and La Palma (Canary Islands). *Proceedings of the Malacological Society of London*, 22(6): 353–354, pls. 18–20.

ODHNER, N. H., 1954, *Vitrina (Guerrina* n.sect.*) cuticula* (Shuttleworth) and its relations. *Proceedings of the Malacological Society of London*, 31(2): 56–63, pl. 4.

PAULUCCI, M., 1878, *Matériaux pour servir à l'étude de la faune malacologique terrestre et fluviatile de l'Italie et de ses îles*. F. Savy, Paris, [1–4] + I–IV + 1–54 pp.

PILSBRY, H. A., 1919, A review of the land mollusks of the Belgian Congo chiefly based on the collections of the American Museum Congo expedition 1909–15. *Bulletin of the American Museum of Natural History*, 40: 1–370.

PILSBRY, H. A., 1946, Land Mollusca of North America (north of Mexico). *Academy of Natural Sciences of Philadelphia Monographs*, 3(2, part 1): frontispiece + I–VI + [VII–VIII] + 1–520.

PONSSA, M. L., 2008, Cladistic analysis and osteological descriptions of the frog species in the *Leptodactylus fuscus* species group (Anura, Leptodactylidae). *Journal of Zoological Systematics and Evolutionary Research*, 46(3): 249–266.

PRENDINI, L., 2000, Phylogeny and classification of the superfamily Scorpionoidea Latreille 1802 (Chelicerata, Scorpiones): an exemplar approach. *Cladistics*, 16: 1–78.

QUICK, H. E., 1960, British slugs (Pulmonata; Testacellidae, Arionidae, Limacidae). *Bulletin of the British Museum (Natural History), Zoology*, 6: 103–226, pls. 1–2.

RÄHLE, W., 1980, Land- und Süsswassermollusken von Kephallinia und Zakynthos (Ionische Inseln). *Archiv für Molluskenkunde*, 110(4–6): 199–224.

RIEDEL, A., 1980, *Genera Zonitidarum. Diagnosen supraspezifischer Taxa der Familie Zonitidae*

(Gastropoda, Stylommatophora). Backhuys, Rotterdam, 197 pp.

RONQUIST, F. & J. P. HUELSENBECK, 2003, MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19(12): 1572–1574.

SCHILEYKO, A. A., 1986, Sistema i filogeniya Vitrinidae (Gastropoda Pulmonata). *Trudy Zoologicheskogo Instituta Leningrad*, 148: 124–157.

SCHILEYKO, A. A., 1991, Vodrosy filogenii vysšich Pulmonata [Problems of the phylogeny of higher Pulmonata]. *Ruthenica*, 1(1–2): 3–16.

SCHILEYKO, A. A., 2002, Treatise on recent terrestrial pulmonate molluscs. Part 9. Helicarionidae, Gymnarionidae, Rhysotinidae, Ariophantidae. *Ruthenica*, Suppl. 2(9): 1167–1307.

SCHILEYKO, A. A., 2003, Treatise on recent terrestrial pulmonate molluscs. Part 11. Trigonochlamydidae, Papillodermidae, Vitrinidae, Limacidae, Bielziidae, Agriolimacidae, Boettgerillidae, Camaenidae. *Ruthenica*, Suppl. 2(11): 1467–1626.

SIMROTH, H., 1891, Die Nacktschnecken der portugiesisch-azorischen Fauna in ihrem Verhältnis zu denen der paläarktischen Region überhaupt. *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum*, 56: 201–424, pls. 9–18.

SOLEM, A., 1979, Some mollusks from Afghanistan. *Fieldiana Zoology, New Series*, 1: I–VI + 1–89.

SOÓS, L., 1917, Zur systematischen Anatomie der Ungarischen Pulmonaten. *Annales Historico-Naturales Musei Nationalis Hungarici (Zool.)*, 15: 1–165.

SOÓS, L., 1924. Explorationes zoologicae ab E. Csiki in Albania peractae, XXIII. Mollusca. *A Magyar Tudomanyos Akademia Balkan-Kutasainak Tudomanyos Eredmenyei*, 1: 177–197.

SOÓS, L. & H. SCHLESCH, 1924, Notes on some Arctic Mollusca from Greenland. *Annales Musei Nationalis Hungarici*, 21: 94–104.

STABILE, G., 1859, Description de quelques coquilles nouvelles ou peu connues. *Revue et Magasin de Zoologie Pure et Appliquée Série II*, 7: 1–14, un-numbered plate with 23 figs.

STABILE, G., 1864, Mollusques terrestres vivants du Piémont. *Atti della Società Italiana di Scienze Naturali*, 6: 1–141, 1–2 pls.

SWOFFORD, D. L., 2003, *PAUP*: Phylogenetic Analysis Using Parsimony, Version 4. beta 10.* Sinauer Associates, Sunderland, Massachusetts.

TARGIONI TOZZETTI, A., 1873, Vertebrati e molluschi osservati o raccolti in una escursione pel Casentino. *Atti della Società Italiana di Scienze Naturali*, 15: 309–372.

TAYLOR, J. W., 1906, *Monograph of the land and freshwater Mollusca of the British Isles*, 3(12): 1–16. Taylor Brothers, Leeds.

THIELE, J., 1931, *Handbuch der systematischen Weichtierkunde.* Erster Band, Teil 2: 377–778. Gustav Fischer, Jena.

THIELE, J., 1933, Die von Oskar Neumann in Abessinien gesammelten und einige andere afrikanische Landschnecken. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*, 134: 280–323, pls. 1, 2.

UMIŃSKI, T., 1968, Brachium copulatorium (?) in *Vitrina pellucida* (Müller). *Archiv für Molluskenkunde*, 98(3–4): 135–137.

VALIDO, M. J., M. R. ALONSO & M. IBÁÑEZ, 1990, La familia Vitrinidae en Canarias. IV. Revisión de las especies de Gran Canaria, con descriptión de 3 especies nuevas (Gastropoda: Pulmonata). *Archiv für Molluskenkunde*, 120 (1–3): 95–114.

VALIDO, M. J., K. GROH, M. IBÁÑEZ & M. R. ALONSO, 1993, La familia Vitrinidae en Canarias. V. El género *Guerrina* (Gastropoda: Pulmonata). *Archiv für Molluskenkunde*, 121(1–6): 117–124.

VALIDO, M. J., M. IBÁÑEZ & M. R. ALONSO, 2000, Estado de conservación de los vitrinidos canarios (Gastropoda, Pulmonata: Vitrinidae). *Revista de la Academia Canaria de Ciencias*, 11(3–4): 245–264.

VERDCOURT, B., 2005, A new species of *Vitrina* (Gastropoda, Pulmonata, Vitrinidae) from Kenya with a discussion of the genus in East Africa. *Basteria*, 69(4–6): 147–156.

WADE, C. M., P. B. MORDAN & B. C. CLARKE, 2001, A phylogeny of the land snails (Gastropoda: Pulmonata). *Proceedings of the Royal Society of London, Series B – Biological Sciences*, 268: 413–422.

WADE, C. M., P. B. MORDAN & F. NAGGS, 2006, Evolutionary relationships among the Pulmonate land snails and slugs (Pulmonata, Stylommatophora). *Biological Journal of the Linnean Society*, 87(4): 593–610.

WAGNER, A. J., 1915, Beiträge zur Anatomie und Systematik der Stylommatophoren aus dem Gebiete der Monarchie und der angrenzenden Balkanländer. *Denkschriften der kaiserlichen Akademie der Wissenschaften mathematisch-naturwissenschaftliche Klasse*, 91: 429–498 + [1–70], 24 pls.

WIENS, J. J., 2005, Can incomplete taxa rescue phylogenetic analyses from long-branch attraction? *Systematic Biology*, 54 (5): 731–742.

WIKTOR, A. & T. BACKELJAU, 1995, Redescription of the Azorean endemic slug *Plutonia atlantica* (Morelet, 1860) (Gastropoda terrestria nuda). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Biologie*, 65: 69–82.

ZHILTSOV, S. S. & T. V. SELIVANOVA, 2000, Histological structure of the distal portion of genitalia in *Troglaegopis mosorensis* (Kuščer, 1933) (Gastropoda: Pulmonata: Zonitidae). *Folia Malacologica*, 8(2): 161–166.

ZILCH, A., 1959, Gastropoda. Euthyneura. Pp. 201–400, in: O. H. Schindewolf, ed., *Handbuch der Paläozoologie*, 6(2). Borntraeger, Berlin.

Revised ms. accepted 29 November 2010